

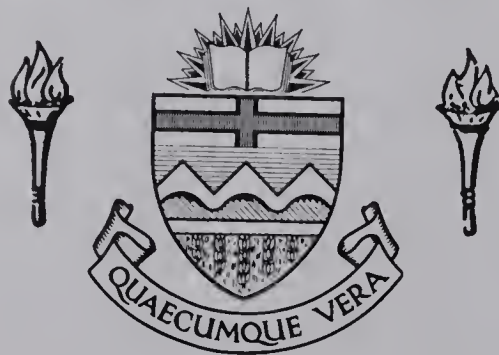
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TRANSIENT ECOLOGICAL SUCCESSION IN A SHALLOW POND

by



GRAHAM R. DABORN

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled Transient Ecological Succession in a Shallow Pond, submitted by Graham R. Daborn in partial fulfilment of the requirements for the degree of Master of Science.

ABSTRACT

An ecological investigation of selected physical, chemical and biological features of a shallow pond was carried out between May 1967 and June 1968. Maximum depth and area of water recorded in May 1967 were 100.6 cm and 0.515 hectares respectively, but as a result of unusually low rainfall and high winds during the study period, the total volume of water in the basin in June 1968 was only 7.1% of that present in May 1967.

Ion concentrations and oxygen saturation of the water increased markedly as ice thickened during the winter, because dissolved and particulate matter was excluded from the ice crystals as they formed. The process is not fundamentally different from that occurring in sea ice. By December 3, 1967, all water in the basin had frozen and remained thus until the end of February, 1968. Ionic concentration in the ice increased at successively greater depths, apparently as a result of the inclusion of water below the ice as freezing occurred. No evidence for the selective involvement of orthophosphate in the ice could be demonstrated.

During the summer months, specific conductance and total hardness increased as water evaporated from the pond, but other physical and chemical features fluctuated irregularly.

A bloom of *Aphanizomenon flos-aquae* was present during June and July, 1967, producing a marked diurnal cycle of oxygen saturation. Gross primary production was estimated at 45 and 30 mg C/m³ per hour over two 12-hour periods (July 4-5, 1967). Thereafter, however, light and dark bottle experiments indicated little or no primary production during the latter part of the summer, and oxygen saturation was considered primarily a function of wind activity and temperature. No bloom occurred in 1968.

Marked changes in faunal composition were recorded in the pond between

1967 and 1968. *Diaptomus leptopus*, *Lumbriculus variegatus* and three species of Coenagrionidae, all of which were common in 1967, were replaced in 1968 by *D. franciscanus*, *Chaetogaster diaphanus* and three species of Lestidae respectively. Distinct changes in relative abundance were also found among the phytoplankton, Rotifera, Ephemeroptera and Diptera between the two summers. These events are interpreted as indicating a temporary acceleration of the process of natural ecological succession, presumably as a result of environmental changes accompanying low rainfall, high sunshine and wind activity.

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Dr. A. D. Hamilton identified certain adult Chironomidae; M. E. Pinsent identified the Mollusca and Lumbricidae; A. D. Nimmo identified the adult Trichoptera; and D. Rosenberg identified the Hemiptera. To these people I express my sincere thanks.

For their companionship and criticism I would like to mention F. Bishop, W. Bond, D. Buchwald, W. Hayden, K. Horkan, M. Paetz, M. Pinsent and K. Zelt.

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INTRODUCTION

The aspen parkland region of western Canada abounds in small, shallow ponds, known locally as 'sloughs', which vary considerably in morphology, permanence and utility. Little is known of these ponds. This is possibly because such bodies of water are frequently of little economic importance and sometimes exhibit a great nuisance value. Their exposed and shallow nature, however, often results in large changes of water volume and temperature during the year. These features in turn represent an interesting ecological situation, since the fauna must be tolerant of such diverse environmental conditions.

When the present study area was first visited on February 5, 1967, it was found that all water in the pond had frozen, but that many organisms embedded in the ice survived on thawing. This phenomenon had been noted before in the arctic (Scholander *et al.*, 1953), but no general ecological study had been conducted on a pond situated in lower latitudes that showed total freezing in winter. Thus, an examination of the seasonal characteristics of this pond was planned.

As the investigation progressed, however, it became obvious that abnormally low precipitation and high summer temperatures had induced marked volume changes in the pond, and that the species composition of the community was also changing. As a result, major emphasis was directed toward the monitoring of these faunal changes. The data thus obtained seem to indicate a temporary acceleration of the process of natural ecological succession.

DESCRIPTION OF THE STUDY AREA

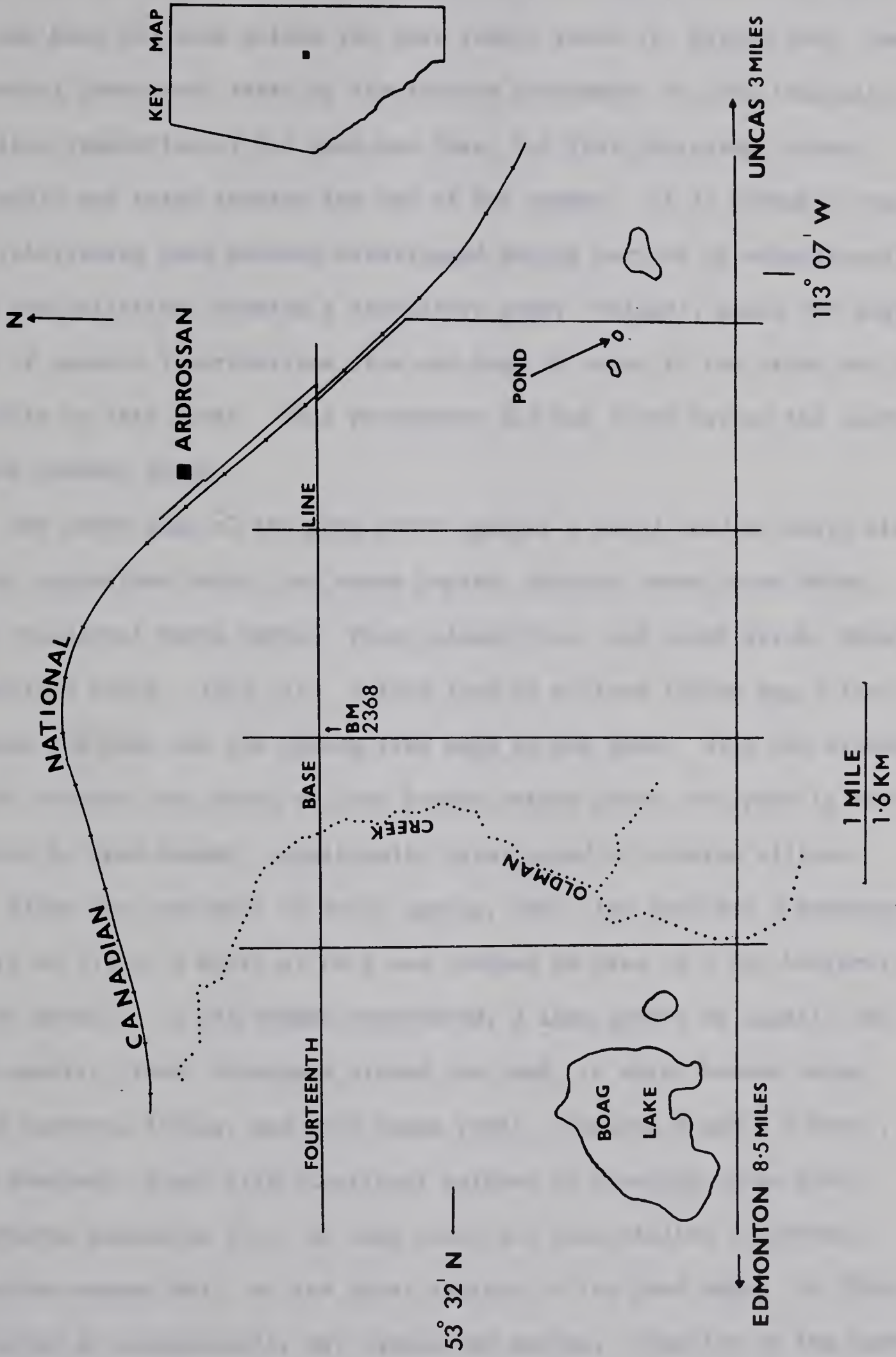
The pond (Fig. 1 and 2) is located approximately 13 miles east of the city of Edmonton in the aspen parkland region of north central Alberta; its geographical coordinates are $113^{\circ} 07' 30''$ west longitude and $53^{\circ} 31' 13''$ north latitude. The surrounding area exhibits a gently rolling topography typical of hummocky dead-ice moraine -- the result of the deposition of till from stagnant ice (Bayrock and Hughes, 1962). The pond itself occupies part of a kettle of this formation. The surface soils of this region have been classified as a mixture of Macola Clay Loam, a dark grey wooded soil of the Podzolic Order; and Mico Silty Clay Loam, an orthic dark grey soil of the Chernozemic series. Both are developed on lacustrine sediments (Bowser *et al.*, 1962).

The climate of the Edmonton region is described as cold temperate, but it is somewhat less severe than might be expected in a continental area at 53°N (Anonymous, 1967). Two thirds of the annual average precipitation of 47.35 cm (18.64 inches) falls during the growing season of spring and summer, but as a result of the drying influence of the Rocky Mountains on maritime Pacific air, the average relative humidity during the summer is lower than elsewhere on the western plains (*Ibid.*, 1967). Variation in the total drying effect of summer weather as represented by wind speed and direction, temperature, humidity and precipitation is an important environmental variable which considerably modifies the seasonal physical characteristics of the pond.

To the west of the pond, lying in the same depression, is a larger lake (Elford's Lake), approximately 300 m long and 100 m wide and separated from the pond by 175 m of low, open meadow. The two bodies of water together drain an area of approximately 50 hectares (20.2 acres). It is

Figure 1. *Map of the study area.*

BM Bench mark



clear that the pond and the lake were once permanently connected, but this has not been the case within the last twenty years (E. Elford pers. comm.). An aerial photograph taken by the Alberta Government in 1950 indicates complete separation of the pond and lake, but this photograph almost certainly was taken towards the end of the summer. It is probable that the intervening area becomes waterlogged during periods of exceptionally high precipitation, forming a transitory water 'bridge'; hence the migration of aquatic invertebrates from one body of water to the other may be possible by this route. This phenomenon did not occur during the course of the present study.

The south edge of the pond abuts against a mixed wood of white birch, *Betula papyrifera* Marsh, and aspen poplar, *Populus tremuloides* Michx., with occasional white spruce, *Picea glauca* Voss, and scrub birch, *Betula glandulosa* Michx., (Fig. 2). A thin line of willows (*Salix* spp.) lies between the wood and the spring-time edge of the pond. With the exception of the eastern end, where willows become rather dense, the pond is surrounded by open meadow, occasionally interrupted by stunted willows.

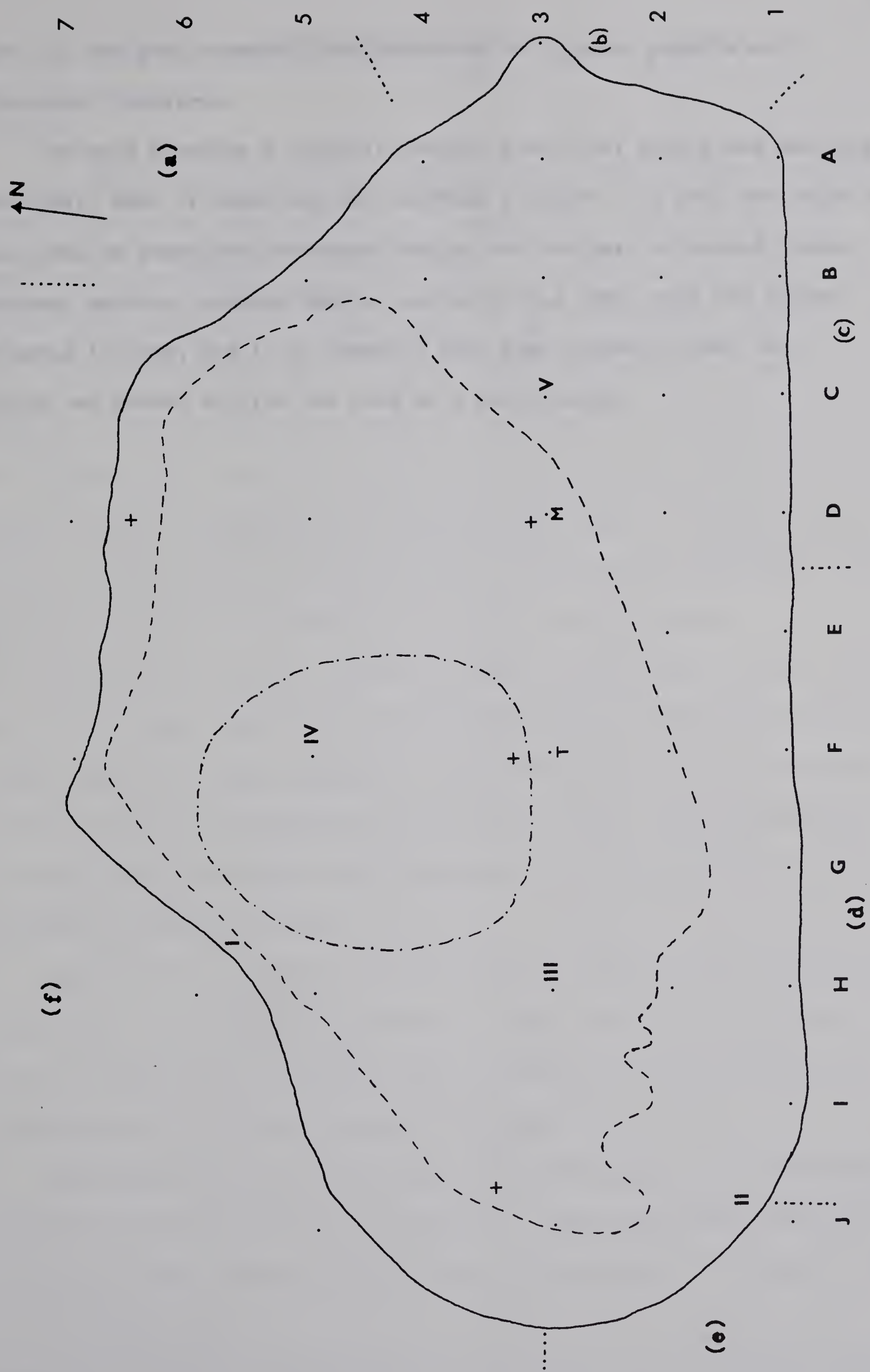
After the snow-melt in early spring, 1967, the pond had a maximum length of 110 m, a width of 60 m and covered an area of 0.515 hectares (1.264 acres). As the summer progressed, a lush growth of aquatic and semi-aquatic plants developed around the pond, in which beaked sedge, *Carex rostrata* Stokes, and tall manna grass, *Glyceria grandis* S.Wats., were dominant, mixed with occasional patches of creeping spike rush, *Eleocharis palustris* (L.), in damp areas and long-stalked chickweed, *Cerastium nutans* Raf., on the drier regions of the pond edge. In 1968, following an exceptionally dry winter and spring, recession of the water level was much more rapid than in the previous summer, and by the end of

Figure 2. *Diagram of the study area.*

·	Location of stake in grid system
A-J; 1-7	Numbering system for grid: at intervals of 10 m
M	Marker post
T	Thermograph position
+	Emergence trap positions
I-V	Sampling points
(a)-(f)	Major vegetation zones
(a)	Scrub - <i>Salix</i> spp.*; <i>Populus tremuloides</i>
(b)	Scrub - <i>Salix</i> spp.*; <i>Populus</i> sp.
(c)	Birch woodland - <i>Betula papyrifera</i> *
(d)	Mixed woodland - <i>Populus tremuloides</i> *, <i>Betula papyrifera</i> *, <i>Picea glauca</i> , <i>Salix</i> spp.
(e)	Mixed woodland and scrub - <i>Betula papyrifera</i> , <i>Betula glandulosa</i> , <i>Salix</i> spp.
(f)	Coarse meadow - <i>Salix</i> spp.

* indicates dominant species of tree.

_____	Edge of open water, May 15, 1967
-----	Edge of open water, October 23, 1967
.....	Edge of open water, June 28, 1968
-. - . - . - . - . - .	Boundaries of major vegetation zones



June the emergent community was dominated by *Glyceria grandis* and *Eleocharis palustris*.

The pond provides a suitable feeding ground for diving and dabbling waterfowl, most of which are only daytime visitors. In 1967 two pairs of coot, *Fulica americana americana* Gmelin, and one pair of horned grebes, *Podiceps auritus cornutus* Gmelin, nested on the pond; only the grebes returned in 1968, and it is doubtful that they nested in that year. Cattle and horses utilise the pond as a water supply.

MATERIALS AND METHODS

Physical

In order to trace seasonal changes in the volume of water in the pond a grid was constructed consisting of wooden stakes placed 10 m or 20 m apart over the southern half of the pond. A few other stakes were inserted on the north side, but the deepest part of the pond remained clear in order that the normal activities of visiting waterfowl would not be disrupted. Since the water receded mainly from the south and east edges where the grid was complete, the network fulfilled its function without disturbing the region in which water persisted throughout the summer. The positions of stakes in this grid are indicated in Fig. 2 and specific locations in the pond are referred to according to the grid numbering scheme.

A one-metre stick was attached to stake D5 and regular records were kept of the "true" depth¹ of water at that point. On March 22, 1968, while a thin layer of ice yet remained on the surface of the water, a complete survey of depths was conducted using a metre stick. These measurements, in association with others taken throughout the study, have been used to estimate the volume of water.

From May 17 until August 12, 1967, water temperature was measured on most visits with a mercury thermometer. Spot checks were also taken in this way during the rest of the study, principally in association with determinations of dissolved oxygen and specific conductance.

On August 12, 1967, a Ryan Model D-30 Thermograph with a temperature range of -5°C to +25°C was installed at F3. This instrument remained in operation, except for two periods of repair (September 12 through 25, 1967;

¹This was defined as the depth of water and loose bottom sediments combined.

January 17 through March 5, 1968) until the end of the project. The chart was changed every 30 days. In order to alleviate problems associated with a falling water level, the instrument was reset each month so that its top surface was at a depth of 16 cm. In winter, the thermograph was cut out of the ice with a chain saw and, after the chart had been replaced, returned to its original location; the hole was then refilled with ice chips and water provided for this purpose. It is assumed that the thermal conductivity of this 'new' ice is not significantly different from the natural ice (Dorsey, 1940).

The turbidity of the lake and ice was determined with a Hach model DR-EL Portable Water Engineer's Laboratory Kit. Ice thickness during the winter was measured with a metre stick.

Chemical

Water samples for regular monthly analysis were taken in the region of F3. Determinations of hydrogen ion, alkalinity, hardness, orthophosphate, sulphate and total nitrate were conducted at intervals of approximately one month of the ice-free season (Table 1) using the Hach Kit. Less frequent determinations of chloride and total iron levels were made using the same instrument. On one occasion, October 26, 1967, additional determinations were made of chlorine, chromate, copper, hydrogen sulphide and silica levels. The specific conductance of the water was measured with a Beckman RB3 Battery Operated Solu Bridge adjusted to 25°C.

Determinations of the above characteristics were also conducted on the ice when this was present. During the period of December 3, 1967, to January 30, 1968, when all water in the pond was frozen, blocks of ice were cut out using a chain saw. In the laboratory the blocks were cut into horizontal sections of approximately 5 cm thickness. Each section was

allowed to thaw in a closed plastic bag before analysis.

At all other times, chemical determinations were carried out in the field.

Analysis of dissolved oxygen was conducted using the Alsterberg modification of the Winkler Method (A.P.H.A., 1960). Water samples were obtained using a one-litre Kemmerer bottle; during the periods of low water in summer this instrument had to be inserted at an angle and closed by hand while in a horizontal position. Samples were taken at three-hour intervals for a total period of 24 hours each month of the ice-free season from July 1967 through May 1968 (Table 1). In June 1968 the very low water level prohibited use of the Kemmerer bottle, and determination of dissolved oxygen was omitted.

Biological

For the examination of plankton, 10-litre samples of water were taken by dipping a two-litre beaker under the surface of the water five times, and pouring this through a Wisconsin plankton net lined with #20 bolting silk. The sample was then washed directly into a bottle and the volume made up to 200 ml with 10% formalin. In the laboratory each sample was thoroughly shaken and a 5.0 ml subsample drawn out into a hypodermic syringe and expelled into a Wild 5.0 ml chamber. The subsample was allowed to settle before examination with a Wild M40 inverted stage microscope using low-power (60X) magnification. All zooplankton were counted by this method. Estimates of phytoplankton numbers were obtained by drawing ten 1.0 ml subsamples into a tuberculin syringe and emptying this into a cavity slide for observation under 600X magnification; counts for 20 random fields were made and a correction factor (29.52) applied to obtain an estimate of the number of cells per 1.0 ml of subsample. Neither of the above techniques

Table 1. *Summary of visits to pond and sampling programme.*

CW	- Turbidity and chemical tests on water
CI	- Turbidity and chemical tests on ice
D	- Dip net sample
ED	- Ekman grab sample
ET	- Emergence trap sample
GC	- Garbage can sample
I	- Ice sample
LD	- Light bottle-dark bottle test
O	- 24-hour oxygen series
(O)	- Single oxygen determination
P	- Plankton sample
VS	- Vertical sample

Date		CW	CI	D	ED	ET	GC	I	LD	O	(O)	P	VS
<u>1967</u>													
Feb.	5							x					
May	17												
	18												
	19				x	x	x						
	21					x							
	24					x	x						
	26					x							
	27	x											
	29			x		x							
	31			x		x						x	
June	2			x		x							
	6					x							
	8					x							
	13					x							
	16					x							
	20	x		x	x	x	x				x		
	24					x							
	27					x					x	x	
	29					x						x	
July	3					x							
	4					x			x	x		x	
	8					x							
	11					x							
	13					x							
	16					x							
	19					x							
	22					x							
	24	x				x			x	x		x	x
	29					x							
Aug.	1					x							
	3					x							
	6					x							
	9					x							
	12					x							
	15					x							
	19					x							
	22					x							
	25					x						x	
	26												
	27												
	28	x				x			x	x		x	x
Sept.	20												
	28	x				x			x	x		x	x
	30					x							

Table 1 (continued):-

Date	CW	CI	D	ED	ET	GC	I	LD	O	(O)	P	VS
Oct. 3					X							
6					X							
10					X							
13					X							
17					X							
20					X							
25					X							
26	X							X	X		X	X
Nov. 1												
5	X											
7	X	X								X		
13	X	X								X		
21	X	X								X		
28	X	X					X			X	X	X
Dec. 9							X					
29												
30							X					
<u>1968</u>												
Jan. 16												
18												
30							X					
Feb. 27												
Mar. 6	X		X							X		
22	X	X	X				X					
Apr. 3	X		X							X	X	
10			X									
19	X											
25	X		X	X				X	X		X	X
May 3					X							
7					X							
11					X							
14					X							
17			X	X	X							
21			X		X							
25			X		X							
29	X		X		X			X	X		X	X
June 4			X		X							
8					X							
12					X							
15					X							
19					X							
24	X				X						X	X
28					X					X		

is standard (Kutkuhn, 1958), and no estimate of reliability can be given. It is assumed, however, that the results are sufficient to indicate seasonal trends, which was the original purpose.

A wide variety of instruments and techniques have been devised for quantitative or semi-quantitative sampling of lake fauna, and some of these techniques have been reviewed by Cummins (1962), who commented that the number of samplers is nearly proportional to the number of investigators. Clearly, this diversity of methods is partly a function of the variation in purpose for which sampling methods may be required, and partly a response to special conditions pertaining to each study area (Southwood, 1966). The standard Ekman grab (*Ibid*; Welch, 1948) was rejected in the present study for two reasons: (i) in the centre of the pond it would sample only the bottom fauna, omitting that portion of the pond community occupying the overlying water; (ii) when used among emergent vegetation the instrument is subject to interference by the plants themselves. Many other techniques (e.g., Jenkin and Mortimer, 1938; Livingstone, 1955; Vallentyne, 1955; Brown, 1956; Elgmork, 1962; Brinkhurst, 1967) fail to answer at least the first of these requirements. Gerking's technique (1957), although designed to sample both the water column and the sediments, could not be used because in early spring the water was too deep in the centre of the pond.

In order, therefore, to sample all regions of the pond in a uniform manner, a new sampler was devised (Fig. 3). It consisted simply of a hollow metal cylinder, 1 m in length, with an area of cross-section of 102.88 cm^2 and a diameter of approximately 11.45 cm. The rim of one end was sharpened and handles were affixed to the other. At a distance of 1 cm from the lower (sharpened) end a horizontal *holding bar* was inserted

Figure 3. *Diagrammatic outline of the vertical sampler.*

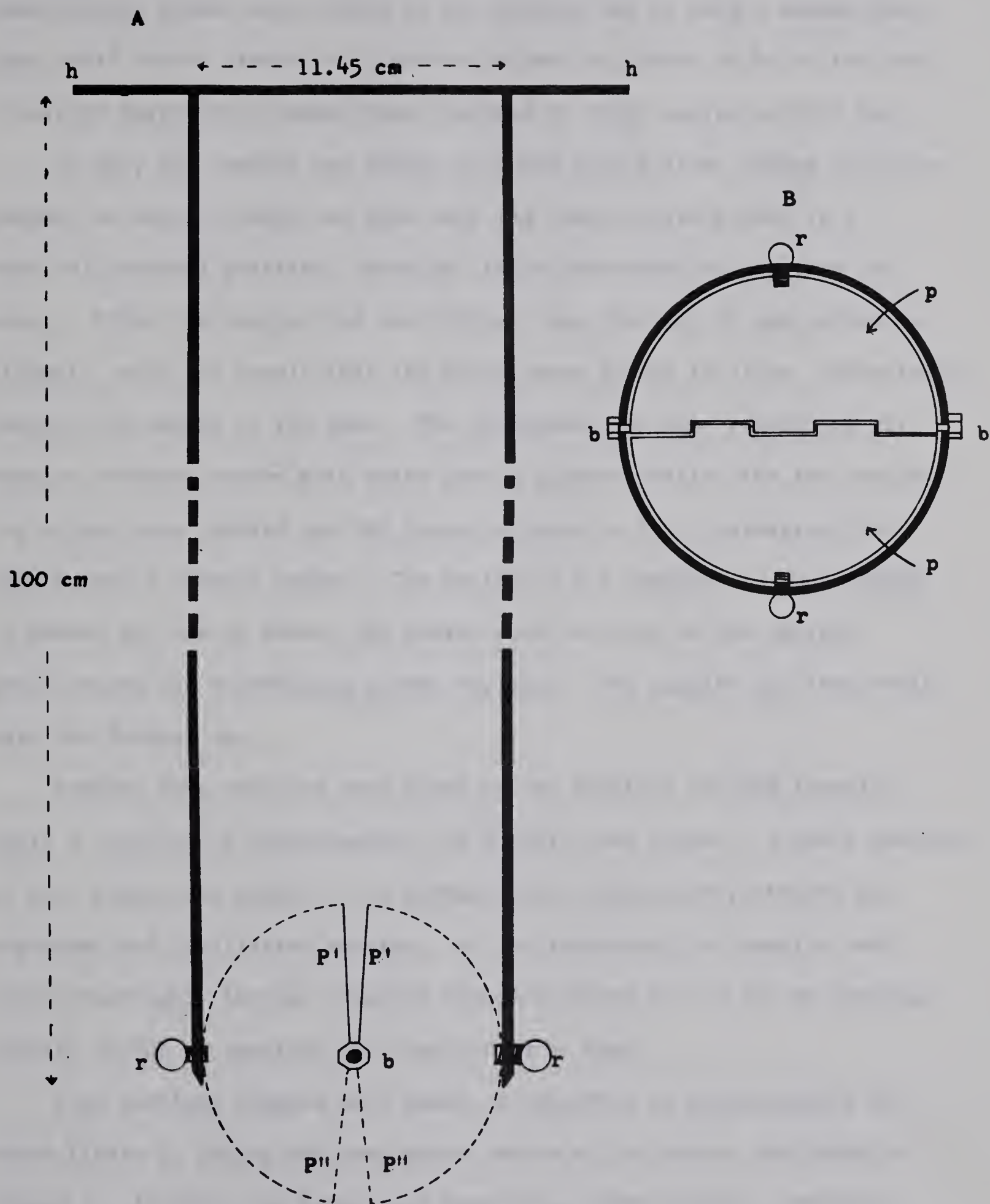
- A. *Side view with positions of the semicircular plates during sampling (P') and emptying (P'') indicated.*
- B. *End view showing articulation of semicircular plates on the holding bar; the plates are indicated in the closed position.*

h - handles

b - holding bar and nuts

r - restraining screws

p - semicircular plates



across the diameter of the tube and held firmly by two nuts. A pair of *semicircular plates* were fitted to the holding bar in such a manner that they could rotate freely in a vertical direction, above or below the bar. A pair of *restraining screws* were inserted at right angles to this bar.

In use, the sampler was thrust into the pond bottom, during which the passage of water through the tube kept the semicircular plates in a vertical (upward) position, offering little resistance to the flow of water. After the sampler had been driven into the mud, it was pulled up slightly, with the result that the plates were forced to close, effectively sealing the sample in the tube. The instrument was then raised and all outside surfaces washed with water from a squeeze-bottle; the two restraining screws were removed and the plates allowed to fall, releasing the sample into a plastic bucket. The inside of the sampler was then washed to remove any mud or fauna, the plates were returned to the upright position and the restraining screws replaced. The sampler was then available for further use.

Samples thus obtained were fixed by the addition of 100% formalin until a solution of approximately 10% formalin was formed. A small quantity of rose bengal was added to the formalin which effectively stained the organisms and facilitated sorting. In the laboratory the samples were washed thoroughly through Canadian Standard sieves #20 (0.841 mm opening) and #30 (0.595 mm opening) and then sorted by hand.

Five vertical samples were taken at intervals of approximately one month (Table I) during the open-water season at the points indicated in Figure 1. In April, an Ekman grab sample was taken beside a vertical sample at station IV, while the vertical sampler remained in position. The results for both samples are tabulated in Appendix II. From a direct

comparison of the number of Chironomini in each sample it is concluded that the vertical sampler is a reasonably satisfactory semi-quantitative method.

From November 1967 to March 1968 this technique was rendered inoperable by the presence of ice, but organisms contained in ice blocks taken for chemical analysis (see above) were kept and enumerated. On March 22, 1968, samples were taken using a dip-net with 11.8 meshes per cm in order to compensate for the absence of vertical samples for that month. In subsequent weeks the dip-net was also used to obtain specimens of *Eubbranchipus* (=Chirocephalopsis) *bundyi* Forbes and *Lynceus mucronatus* (Packard); such samples were taken at intervals of 4 to 7 days (Table 1).

Throughout the ice-free season the emergence of aquatic insects was monitored using floating box-frame traps (Morgan and Waddell, 1961; Morgan, Waddell and Hall, 1963). Each trap consisted of a cedar wood frame covered on the top and all sides with nylon netting (11.8 meshes/cm) and enclosing an area of 0.093 m² (1.0 ft²). The trap was supported in the water by a floating raft, and was emptied by sliding a board beneath the opening, under the surface of the water, and transferring the whole to a boat or to land. Any pupae or adults which remained on the surface of the water within the confines of the raft were immediately placed in a vial of 70% ethanol and considered part of the catch. The trap and its contents were then sprayed with a commercial insecticide and left for five minutes, after which the catch could be removed without loss. These traps were emptied every two to four days in 1967 and every four or five days in 1968 (Table 1). The merits and limitations of this kind of trap have been discussed by Southwood (1966). The results obtained in the present study are considered non-quantitative.

PHYSICAL CHARACTERISTICS

It was apparent from the beginning of the study that seasonal changes in the physical characteristics of the pond would be extensive, and perhaps exert considerable influence on the biotic community. The most dramatic changes were those associated with recession of the water during summer and the freezing of the pond in winter.

Morphometric Variations

When the pond was first visited in May 1967, after the spring snow-melt, it was roughly subcircular (Fig. 2) with a maximum length of 110 m and a maximum width of 60 m. This area of open water was surrounded by a marshy region varying in width from 1 m (south edge) to 15 m (east edge), which rapidly dried out as the season progressed. With increasing air temperatures and an exceptionally low rainfall (Fig. 5) the water diminished in area and volume until, in October 1967, it covered less than half of the spring-time area and was less than one-quarter of its former volume. The water receded mostly from the south and east edges where it appears that sediments have accumulated at a greater rate than elsewhere -- presumably under the influence of predominantly westerly or northerly winds. It is certainly significant in this connection that the pond is exposed both to the west and to the north.

In April 1968 the water extended almost to the previous spring level, but during the summer a rapid shrinkage occurred so that at the end of July only a small area in the deepest part of the basin contained water (Fig. 2). These changes are summarised in Table 2. The appearance of the pond in early spring and in the autumn of 1967 is shown in Figure 4.

While it is clear that such major variations were the result of an

Figure 4. A. *The pond in May 1967 -- from the east edge*

B. *The pond in October 1967 -- from the east edge*



Table 2. *Changes in morphometric characteristics of the pond during the study period*

Date	Depth at D3 (cm)	Maximum Depth (cm)	Area (m ²)	Volume (m ³)	% Area* Reduction	% Volume* Reduction
May 22, 1967	71.6	100.6	2,735	2,247.5	-	-
October 23, 1967	23.0	52.0	1,825	561.25	32.3	75.03
June 28, 1968	12.5	41.5	550	159.5	79.9	92.9

*Compared with May 22, 1967

exceptionally low precipitation during 1967, it is considered probable that extensive seasonal changes occur in the volume of water in the pond in most years. The biological implications of this feature are difficult to assess in detail. It may be postulated here, however, that the effects of decreasing water volume -- closer correspondence of water temperature with air temperature, early onset of freezing in winter, the necessity for most of the fauna to avoid the edges of the pond which are drying out and the associated increase in the faunal density in the remaining water, for example -- may be important factors limiting the stability of the community from one year to the next.

Temperature

In general, water temperatures followed those of the air² (Fig. 5) with average diurnal variations of approximately 3-5 C°; these diurnal fluctuations were much more pronounced in May and June 1968, presumably as a result of the extremely low water level. It is clear from Figure 5 that the formation of the first permanent ice cover (November 3, 1967) had a marked effect in reducing the otherwise close correspondence between water and air temperatures. Diurnal changes were eliminated initially, but subsequently reappeared when the pond had frozen to the bottom. This is undoubtedly a result, in part, of the lower thermal conductivity across an ice-water interface than through ice itself (Dorsey, 1940); but it may also be a function of the variation in snow depth covering the ice (Scott and Ragotzkie, 1961; Scott, 1964). The high albedo and low thermal conductivity

²The air temperature and precipitation data included in Figure 5 are those recorded at the Industrial Airport, about 15 miles west of the study area. The air temperatures are thus only approximations of those occurring at the study area.

Figure 5. *Summary of air and water temperatures, precipitation and ice cover during the study period, May 1967 to June 1968*

Top: Daily range of air temperature recorded at
Edmonton Industrial Airport

Middle: Water temperatures and ice cover

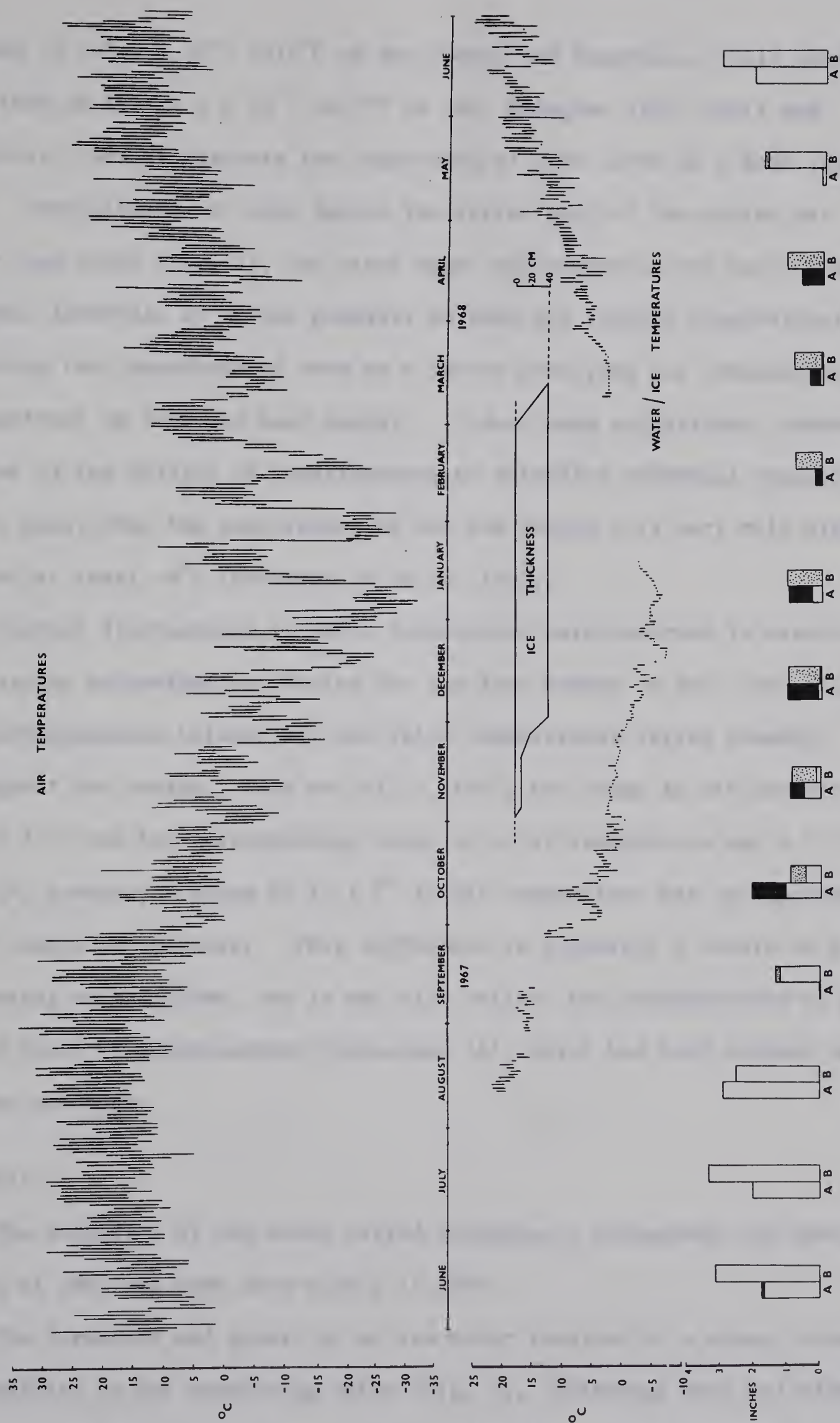
Bottom: Monthly precipitation recorded at Edmonton
Industrial Airport

A. 1967-1968 values

B. Long-term average values (1894-1967/8)

Snow : shaded

Rain : clear



of snow ($0.7-1.0 \times 10^{-4}$ cal/°C cm sec, Scott and Ragotzkie, 1961) compared with that of ice (5.0×10^{-3} cal/°C cm sec, Malmgren 1927; Scott and Ragotzkie, 1961) illustrate the importance of snow cover as a heat insulator. Precipitation as snow during the latter part of the winter was lower than usual (Fig. 5), but since depth measurements were only taken at sporadic intervals it is not possible to make any further observations regarding the importance of snow as a factor modifying ice temperature, or to construct an adequate heat budget. It does seem significant, however, in view of the ability of invertebrates to establish perennial populations in the pond, that the temperature of the ice during this very mild winter reached at least -8°C (December 19 to 23, 1967).

Diurnal fluctuations in water temperature were recorded in association with oxygen determinations during the ice-free months in each year (Fig. 6). The correspondence between air and water temperatures varied somewhat throughout the season. Thus on July 4, 1967, the range in air temperature was 12.3°C and the corresponding range in water temperature was 6.5°C . On July 24, however, a range of 15.1°C in air temperature was accompanied by a 12.5° change in the water. This difference is primarily a result of the decreasing water volume, but it may also reflect the disappearance of a severe bloom of *Aphanizomenon flos-aquae* (L), which had been present on the earlier occasion.

Turbidity

The turbidity of the water varied irregularly throughout the open-water season of 1967 and even more widely in 1968.

The formation and growth of an ice cover resulted in a sharp increase in turbidity in the underlying water (Fig. 7), indicating that colloidal and suspended particulate matter tends to be eliminated from water which is

Figure 6. *Diurnal fluctuations in water temperature*

N Noon

M Midnight

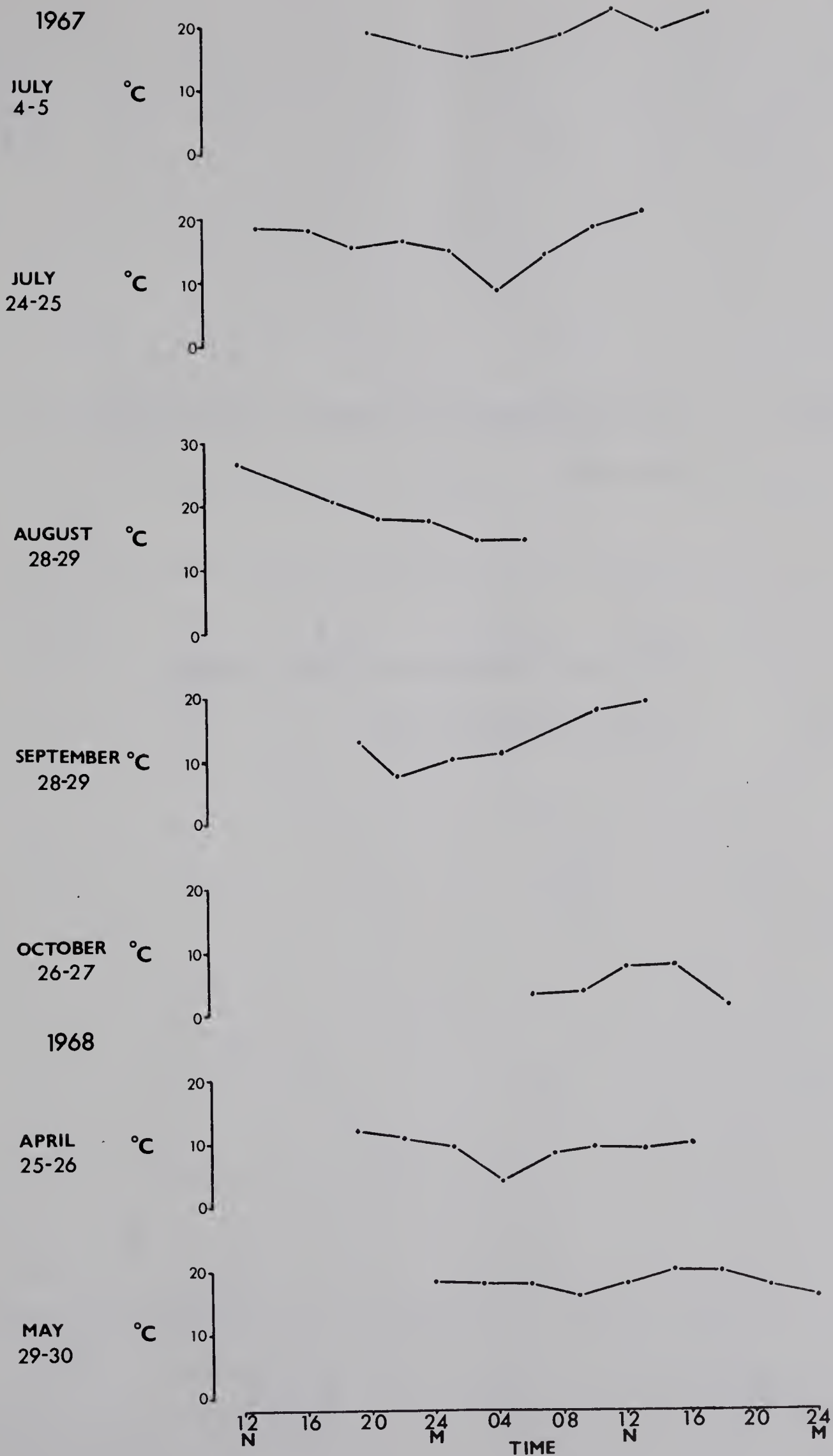


Figure 7. *Selected physical and chemical characteristics of
the water*

— — — — — Indicates intermediate value(s) missing
JTU Jackson Turbidity Units

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changing state. As the ice thickness increased, this process of exclusion of suspended matter appeared to be less complete and the turbidity of the ice became greater at lower depths. As will be demonstrated in a later section this phenomenon applies equally to all other ions and is undoubtedly the reason for the analogous absorption spectra of natural ice and water in the wavelength range of $6,000\text{\AA}$ to 6μ (Dorsey, 1940). One important feature of this elimination is that the first-formed ice contains fewer particles to act as radiation absorbers and therefore is less subject to internal melting (Tyndall, 1898; Scott and Ragotzkie, 1961; Scott, 1964).

Ice History

In the winter of 1967-68 ice was first recorded at the edge of the pond on the night of October 24, and for several days thereafter an intermittent ice cover was present at night, which subsequently thawed during the day. The process of ice formation in shallow waters is well known (Dorsey, 1940): currents of warm air rise from the centre of the pond drawing colder air in from the sides which cools and ultimately freezes the water at the edge. The first permanent ice cover was formed apparently on November 3, 1967, and within two days had reached a thickness of 8.0 cm. It was noted that this first ice was quite transparent. On November 21 the same thickness of ice was recorded, but one week later it had increased to 20 cm and by December 3 only the bottom sediments remained fluid. The temperature of this mud was 0.8°C . By the end of December the pond was totally frozen and attempts to find wet mud were unsuccessful.

Unusually warm periods occurred in January and February, 1968, during which the snow and perhaps part of the ice surface thawed and refroze, but the remainder of the pond remained solid. Spring break-up began at

the end of February (an unusually early time) and melting occurred first at the surface of the ice. Periodic refreezing at the surface took place on cooler nights, but by March 6 all but the bottom sediments had thawed. This situation continued until the beginning of April, the mud being covered by 2 cm of ice and 40 cm of water. The continued presence of ice at the bottom of the pond is attributed to the existence of particulate matter in the lower layers of the ice overlying the mud when melting began: the particles acted as 'black body' absorbers, thereby removing much of the incident light energy before it could penetrate to the bottom. The importance of solar radiation rather than air temperature in the melting process was indicated by the persistence of ice along the southern edge of the pond, which lay in the shadow of the trees.

Ice Cores

In association with chemical determinations and turbidity measurements ice cores were taken from the pond on three occasions during the winter, and notes were made on the appearance of the ice at different levels. As mentioned above, the first-formed permanent ice was transparent (November 5, 1967), but the top layer of ice in a block obtained on December 9, 1967, was cloudy or "bubbly". This was presumably the result of the freezing of slush derived from partial melting of snow, and in this connection it may be noted that 6.35 cm (2.5 inches) of snow fell on November 11, but by November 15 only 2.54 cm (1 inch) remained on the ground. The maximum air temperatures recorded for the period November 11 to 15 were 0.6, -2.2, 1.7, 2.8 and 9.5°C respectively.

Below this layer of cloudy ice (0.0-6.5 cm) a band of clear ice occurred with no bubbles but with a distinct brown colouration, which increased in strength at successively deeper levels. The presence of this

colour would appear to indicate progressively greater involvement of soluble, colloidal and other particulate matter in the ice as it increased in thickness.

Light penetration through ice is greatly diminished by the presence of both bubbles and other inclusions. Greenbank (1945) records that 84% of incident light was transmitted through 7.5 inches (19.05 cm) of clear ice compared with 22% through the same thickness of partly cloudy ice. With respect to the process of thawing in the pond, therefore, it is apparent that most of the incident solar radiation in February would have been absorbed in the upper layers of the ice, and would not have penetrated to the bottom.

These profound changes in the physical nature of the pond obviously represent significant features of the environment which must exert considerable influence on the nature of the biotic community. Thus, it has been shown that the aquatic fauna is subjected to extensive reduction in the volume of the pond during the summer, wide diurnal and seasonal fluctuations in water temperature, total freezing of the water in winter and ice temperatures which fall considerably below 0°C. It is not possible at the present time to relate these environmental conditions to the specific composition of the pond fauna and flora, but it is considered highly probable that this degree of variability in the environment contributes greatly to the instability of the biological community.

CHEMICAL CHARACTERISTICS

The chemical composition of natural water is determined by a multitude of factors acting independently or in concert, and thus any measurement of ionic concentration represents merely the end product of a complex series of actions and reactions. In a closed lake basin, ionic concentration is increased by evaporation and the introduction of additional nutrients by ground water, and may be decreased by atmospheric precipitation. Since the latter may be regarded as the antithesis of evaporation, changes in the inorganic composition of water in a closed lake system are primarily a function of the equilibrium states established between ground water and the soils through which it flows. Natural standing waters may therefore be considered "integrators" of environmental chemical activity in the same way that they are considered integrators of climate (Scott and Ragotzkie, 1961; Scott, 1964). It is possible, however, to distinguish between the respective importance of these major determinants of ionic composition for a specific lake on an *a priori* basis (Rawson, 1942; Hutchinson, 1957).

Open Water Season 1967 and 1968

During the course of this study the pond received no appreciable inflow of water other than atmospheric precipitation and ground seepage from the drainage basin, and produced a slight effluent only for a period of one week in May 1967. It is considered, therefore, that the major influences on chemical composition during the open-water season were precipitation, evaporation, influx of water from ground seepage and, perhaps, the seasonal development of autotrophs. Of these factors precipitation in 1967 was lower, in many areas, than the capacity of the soil to retain moisture for its own use, and, therefore, no surplus was available to

provide surface or ground water seepage (Laycock, 1968). Thus, total precipitation for the months of May through November 1967 was 27.4 cm (10.8 inches), and if it may be assumed that the pond received only that precipitation falling on its maximum area (probably an overestimate), the contribution of water by precipitation during this period was 750 m³ compared with almost 2500 m³ that evaporated from the pond during the same period. It is clear, therefore, that evaporation was a much more important factor than precipitation.

The fourth factor, that of the seasonal development of micro- and macrophytes, was not investigated in this study. It is considered probable, however, that it is of great significance in the determination of ionic composition.

The results for each ion measured at monthly intervals, and for specific conductance, hydrogen ion concentration and turbidity, are presented graphically in Figure 7.

Hardness, Alkalinity and Specific Conductance

During the summer of 1967 the total hardness of the water increased steadily from 82 ppm on July 24 to 153 ppm by October 26. This rise in concentration was undoubtedly a function of evaporation. In the first months of open water in 1968 a similar upward trend was apparent.

The calcium hardness:magnesium hardness ratio (Table 3) varied somewhat throughout the summer, around a mean of 1.49. This value is considerably lower than those (5.5-6.5) given by Rodhe (1949) for a 'standard bicarbonate water', but lies in general conformity with results obtained for waters of Alberta by Rawson (1942), Kerekes (1965), and Pinsent (1967). In hard waters such as in this pond, a general increase in the proportion of magnesium to calcium is common (Hutchinson, 1957; Reid, 1961),

Table 3. Comparison of specific conductance, and total, calcium and magnesium hardness values, 1967-68

Date	S.C. µmhos	S.C. ppm	Tot. H.	% S.C.*	Ca.	% S.C.*	Mg.	% S.C.*	Ca:Mg.
<u>1967</u>									
Aug. 28	195	109.2	110	100	55	50	55	50	1.00
Sept. 28	310	174.0	130	74.8	85	48.9	45	25.9	1.89
Oct. 26	300	168.0	153	91.1	90	53.6	63	37.5	1.43
Nov. 5	380	212.8	189	89.3	121	56.9	68	32.4	1.78
" 13	390	218.4	213	97.5	125	57.2	88	40.3	1.42
" 21	485	271.6	246	90.5	153	56.3	93	34.3	1.65
" 28	850	476.0	481	100	261	54.8	220	45.2	1.19
<u>1968</u>									
Mar. 6	185	103.6	57	55.0	28	27.0	29	28.0	0.97
" 22	225	126.0	74	58.7	37	29.4	37	29.4	1.00
Apr. 3	230	128.8	78	60.6	46	35.7	32	24.9	1.44
" 19	260	145.6	100	68.7	59	40.5	41	28.2	1.44
" 26	270	151.2	111	73.4	69	45.6	32	27.8	2.16
May 29	360	201.6	155	76.9	94	46.6	61	30.3	1.54
June 24	265	148.4	113	76.1	75	50.5	38	25.6	1.97

*Previous value expressed as per cent of specific conductance in ppm

apparently at the expense of sodium and potassium.

A general tendency toward increase in the Ca:Mg hardness ratio was apparent for March and April 1968; this may be associated with the seasonal development of macrophytes in the pond.

The alkalinity of the water in 1967 was predominantly a function of the bicarbonate ion (Fig. 7). Normal carbonate (as indicated by phenolphthalein alkalinity) was recorded only on isolated occasions at a maximum level of 10 ppm, but since at all times (except March 1968) the pH remained above 8.4, at which appreciable carbonate is usually present (Hutchinson, 1957), the determinations are probably unreliable and have been omitted. The fluctuations in total alkalinity that occurred in September and October 1967, before ice formation began, and the sudden decrease in June 1968, following a steady rise in concentration in the previous months, are unexplained.

Since calcium and magnesium are the dominant cations present (Table 3) it would be expected that total alkalinity would parallel changes in total hardness : there was, in fact, no correlation in 1967 ($r=0.58$), but a strong correlation in 1968 ($r=0.98$). This is difficult to explain.

Specific conductance (in micromhos) was first determined at the end of August 1967 and thereafter at intervals of one month or less when the pond was free of ice. The general pattern for specific conductance approximates to that of total hardness in both years and in 1968 to bicarbonate concentration also. If the reasonable assumption is made that most of the dissolved substances are completely ionised (Hutchinson, 1957; Reid, 1961; Macan, 1963; Hartland-Rowe, 1966), the total ionic concentration in ppm is approximately 56% of the specific conductance at 25°C (Horne, 1967). In fact the relationship is not linear (Rodhe, 1949), but this approximation is reasonably valid for low concentrations. This

conversion factor has been utilised in Table 3.

It is apparent from Table 3 that there is a strong correlation between specific conductance and total hardness throughout the duration of open water. The coefficient of correlation for all months of ice-free water was 0.99.

Hydrogen Ion Concentration

With the exception of March 1968, when the water above the frozen sediments exhibited a pH below 7.0, the hydrogen ion concentration fluctuated between 8.5 and 9.6 during the ice-free season, the mean being 8.95. The increase in June and decrease in July 1967 were probably related to the intense bloom of *Aphanizomenon* observed at this time. In general, however, it would appear that the CO₂-bicarbonate-carbonate buffer system is sufficient to maintain the pH between these restricted limits (Hutchinson, 1957) despite the distinct changes occurring in other chemical characteristics.

On April 26, 1968, in anticipation of a subsequent phytoplankton bloom, water samples were taken from six different points in the pond, and at intervals of three hours from the centre of the pond (F3) to see if spatial or diurnal fluctuations in pH could be detected. The results indicate that at this time no great variation was occurring (Table 4), and this is presumed to be the case for most of the ice-free season. It is probable, however, that distinct and regular fluctuations do occur at the times of phytoplankton blooms, but as mentioned above, this did not materialise in 1968.

Orthophosphate, Sulphate and Total Nitrates

Of all the elements in natural waters, phosphorus is usually considered the most significant ecologically (Hutchinson, 1957), primarily

Table 4. *Variation in pH, April 26, 1968*

Time	Location	pH
19.00	A5	8.54
	D7	8.25
	D6	8.64
	G1	8.48
	G2	8.66
	C1	8.53
	F3	8.74
22.00	F3	8.91
01.00	F3	8.86
04.00	F3	8.53
07.00	F3	8.76
10.00	F3	8.80
13.00	F3	8.64
16.00	F3	8.55

because of its importance in biological pathways. In shallow ponds and the epilimnion of larger lakes the level of phosphate in the water frequently can be attributed to autotrophic activity. The decline from August through October 1967 (Fig. 6) may be an indication of uptake by macrophytes since at this time the quantity of phytoplankton was low. With the onset of freezing, however, the level of orthophosphate increased in the water as the ice became thicker.

The pronounced diphasic pattern of orthophosphate exhibited in 1968 is difficult to account for; the decline in April might be indicative of uptake by developing autotrophs, but its subsequent increase remains unexplained. It may be, however, a correlative of the exceptionally low water level at this time.

Sulphate was the second most abundant cation in the pond throughout the period of the study. The decline in both 1967 and 1968 is thought to be the result of progressive uptake by macrophytes or to reduction to sulphide which accumulated in the bottom mud. Of the two processes, the apparent absence of hydrogen sulphide (Appendix IV) seems to indicate that the latter is less significant.

Estimates of total nitrates were incomplete in 1967. The high level recorded in May 1967, however, may be correlated with the presence of the blue-green algae *Aphanizomenon flos-aquae* and *Anabaena spiroides*, species that may be capable of fixing molecular nitrogen (Hutchinson, 1957; Lin, 1968). If this is true, the low values obtained in 1968 would correspond with the absence of a bloom during that year.

Additional Determinations

Measurements of several other inorganic substances were obtained on a few isolated occasions. Determinations of chloride ion and total iron

concentrations were made regularly in 1968: this information is included in Figure 7. The results of other tests are given in Appendix IV.

Dissolved Oxygen

At the start of the project determinations of dissolved oxygen concentration were conducted on three separate occasions (Table 5). The development of a bloom of *Aphanizomenon* in the latter half of June, however, suggested that oxygen measurements over a period of 24 hours would be more suitable. On July 4 and 5, 1967, a clear diurnal fluctuation was recorded (Fig. 8): the maximum and minimum saturation being 138% (14.35 hrs) and 65% (05.35 hrs). That this high variation was the result of phytoplankton production was indicated by the concurrent light and dark bottle experiments, which gave estimates of gross production of 45 and 30 mg C/m³ per hour over periods of 12 hours (06.00-12.00; 13.00-19.00 hrs respectively) at a depth of 62 cm.

The bloom disappeared between July 16 and 19, and subsequent oxygen series failed to exhibit any degree of diurnal rhythm. The results obtained on July 24-25 are illustrated in Figure 8. Light and dark bottle results on this date indicated no primary production at 10 and 60 cm depths. This arrhythmic pattern recurred each month for the remainder of the ice-free season (Table 6), suggesting that oxygen saturation was primarily a function of temperature and wind velocity during the latter part of the summer. Light and dark bottle results at these times were confusing, and since the low water level made the establishment of uncontaminated samples difficult, the results are considered unreliable.

With the onset of ice formation in November 1967, incidental determinations of dissolved oxygen were made on three occasions, November 7, 13 and 21 (Table 7). The high values obtained are clearly a result of

Table 5. *Dissolved oxygen concentration, May and June 1967*

Date	Time	Water Temp. °C	D.O. ppm	% Saturation
May 27	10.00	21.0	7.6	87
June 20	16.00	20.2	7.7	87
June 27	12.00	20.0	9.6	108

Figure 8. *Diurnal variation in dissolved oxygen, July 1967*

N Noon
M Midnight

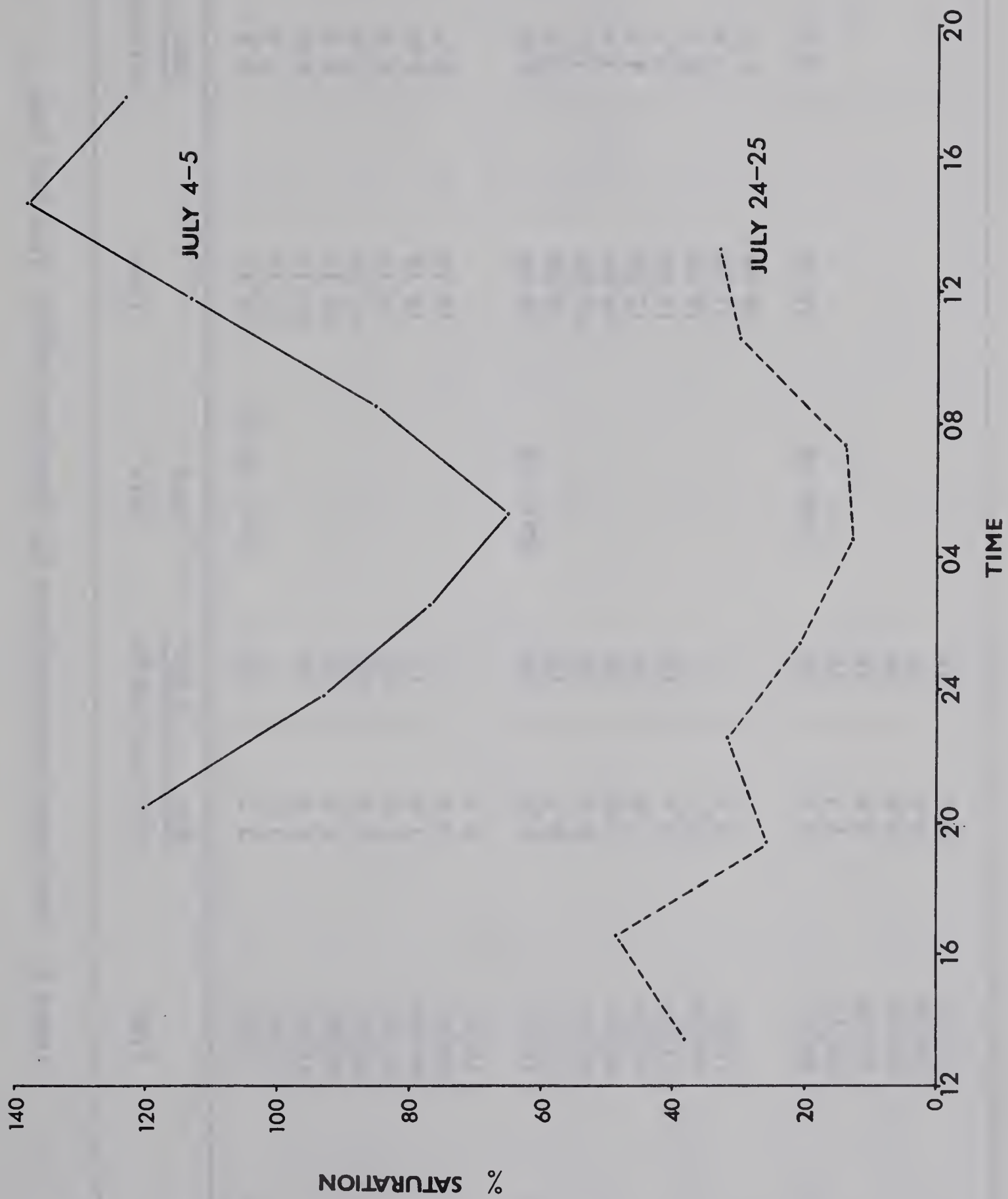


Table 6. Additional determinations of dissolved oxygen, 1967 and 1968

Date 1967	Time	Dissolved Oxygen		Date 1968	Time	Dissolved Oxygen	
		ppm	% Sat.			ppm	% Sat.
Aug. 28-29	12.05	7.7	97	Apr. 25-26	19.15	5.4	52
	15.05	3.2	-		22.15	7.4	68
	18.05	4.9	56		01.15	8.6	78
	20.55	8.2	88		04.15	8.3	64
	00.05	5.2	56		07.20	7.8	69
	03.05	5.9	60		10.15	4.9	45
	06.05	1.8	17		13.15	6.6	58
	09.15	3.8	-		16.10	8.4	77
	12.10	0.3	-				
Sept. 28-29	19.25	8.9	86	May 29	00.00	5.5	58
	21.55	9.2	78		03.00	2.1	23
	01.25	8.1	72		06.00	1.1	12
	04.20	5.9	56		09.00	3.4	35
	10.20	7.6	82		12.00	4.3	47
	13.20	9.6	110		15.00	7.0	80
	16.20	9.5	-		18.00	9.7	110
	19.00	9.8	-		21.00	7.4	78
					24.00	6.1	64
Oct. 26-27	06.15	9.3	70	June 28	04.15	2.5	23
	09.15	7.4	57				
	12.10	8.8	74				
	15.10	10.8	95				
	18.30	9.8	72				
	21.35	10.9	78				

Table 7. . Comparison of physical and chemical characteristics of ice and water, November 1967

Date	7		13		21		28	
Ice thickness	8.0 cm		8.0 cm		8.0 cm		24.0 cm	
Calcium hardness (ppm)	Water	Ice	Water	Ice	Water	Ice	Water	Ice
Magnesium hardness (ppm)	-	-	125	10	153	3	261	16
Total Hardness (ppm)	-	-	88	15	93	6	220	14
pH	-	-	213	25	246	9	481	30
HCO ₃ ⁻ (ppm)	8.84	7.05	8.73	8.32	8.71	6.95	8.74	8.54
Turbidity (JTU)	50.0	2.0	85.0	12.0	102	6	169	15
Orthophosphate (ppm)	35	14	43	28	37	20	64	18
Specific conductance (μmhos)	0.06	0.06	-	-	0.07	0.08	0.34	0.25
Total nitrate (ppm)	400	>50	390	>50	485	>50	850	72
Sulphate (ppm)	2.8	1.4	-	-	2.06	*	5.25	*
Silica (ppm)	22.0	2.0	-	-	-	-	66.0	6.0
Dissolved oxygen (ppm)	-	-	0.49	0.35	-	-	0.59	0.28
Temperature °C	15.05	-	11.25	-	11.41	-	-	-
	2.0						0.8	

*Mauve colour of unknown origin interfered with reading

the freezing process, since ice does not dissolve the oxygen present in the water : instead, as the water reaches supersaturation, dissolved air is released to form bubbles which may then become trapped in the ice (Lliboutry, 1964).

In 1968 oxygen determinations were conducted over 24-hour periods in April, May and June (Table 6). For all three months diurnal patterns were absent, and light and dark bottle experiments (where possible) indicated minimal production : 2 mg C/m³ per hour (April 26) and 0 mg C/m³ per hour (May 29). In June the low water level prevented determinations. The apparent absence of production is clearly correlated with low phytoplankton numbers and the fact that no bloom occurred that year.

From the information obtained it seems safe to conclude that phytoplankton production was restricted almost entirely to a period of little more than one month in early summer. It is possible that this pattern is typical of years in which the water level is higher than that recorded in 1968, but obviously more data are required to establish this.

Winter 1967-68

With the onset of ice formation at the beginning of November 1967, it became obvious that freezing produced marked changes in the chemical composition of the underlying water (Fig. 7). A sharp rise in the concentration of each ion accompanied increases in thickness of the ice cover. In order to monitor these changes more closely samples of ice and water were taken on four occasions between November 7 and 28 and subjected to regular analysis (Table 7).

It is immediately apparent that the freezing of natural inland water is accompanied by the partial exclusion of many inorganic ions. This phenomenon has been widely tabulated with respect to sea ice (Wiese, 1930;

Chernigovskii, 1939; Zubov, 1945; Nelson and Thompson, 1953 and 1954) but with a few notable exceptions (Sparks, 1910; Bartow, 1913; Ruediger, 1913) little work has been conducted on inland waters. Sparks (1910) demonstrated selective exclusion of minerals from ice : the mineral composition of the ice compared with the water prior to freezing was: CaCO_3 1:34.5; CaSO_4 1:6.6; MgCO_3 1:1.4; and MgSO_4 1:1.1. Obviously, calcium was excluded more completely than magnesium and carbonate more completely than sulphate.

If the data for the sample on November 21, 1967, are analysed in the same way, the approximate ice-water ion concentration ratios were : Ca 1:51; Mg 1:15.5; HCO_3 1:17 and SO_4 1:11. The same pattern extends to other constituents, including silica, total nitrate and, perhaps, orthophosphate. The ice-water ratios for orthophosphate were 1:1 (Nov. 7); 1:0.87 (Nov. 21) and 1:1.36 (Nov. 28).

Several inconsistencies are apparent in the specific values obtained for particular ions on the four sampling dates. The low total hardness of ice collected on November 21 does not concur with higher values obtained before and after this date. Since the samples were not necessarily taken from the same point in the pond, it is possible that some of the variation in values is a function of regional differences. In general, however, the selective exclusion of ions from water as it changes state would seem to have been demonstrated successfully.

After all water in the pond had frozen (by December 3, 1967) ice cores were taken in order to examine the vertical distribution of ions in the ice. The results obtained for samples taken on December 9 and 30, 1967, and January 30, 1968, are presented graphically in Figures 9 to 14.

The distribution of ions in the first sample obtained (Fig. 9) seems to indicate two important features of the freezing process in natural water. In the first place, exclusion of ions did occur as demonstrated

Figure 9. *Variation in physical and chemical characteristics of
ice, December 9, 1967.*

JTU Jackson Turbidity Units

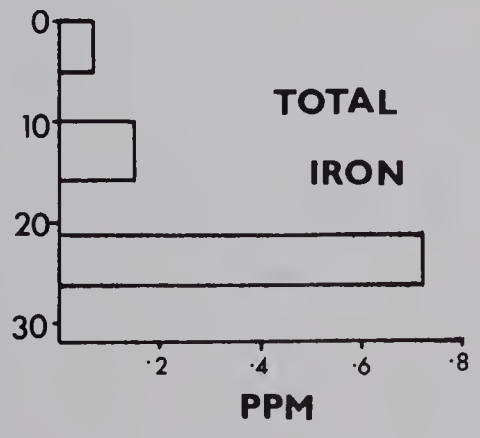
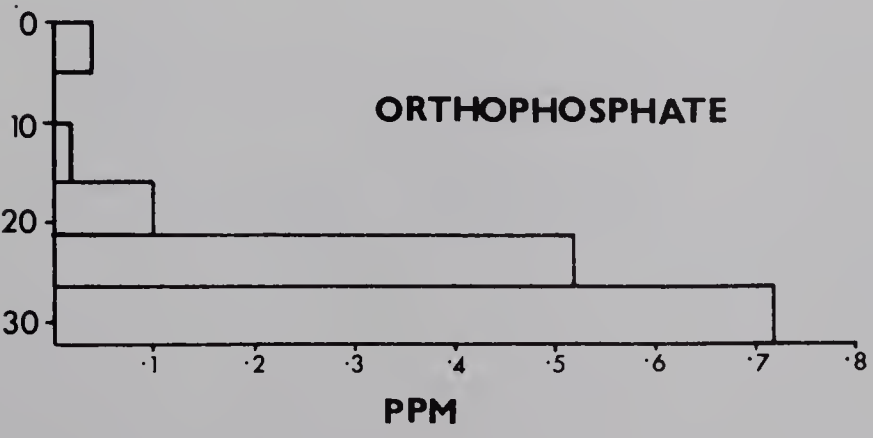
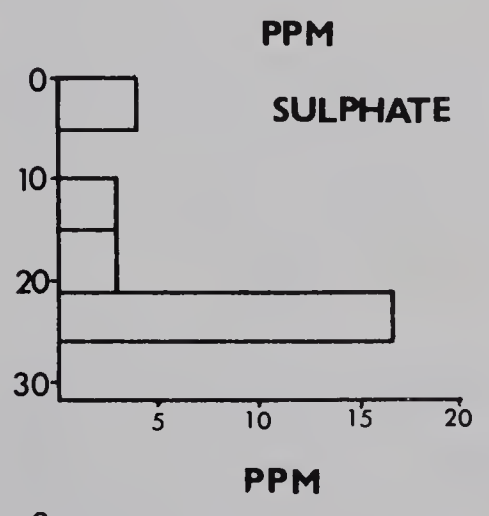
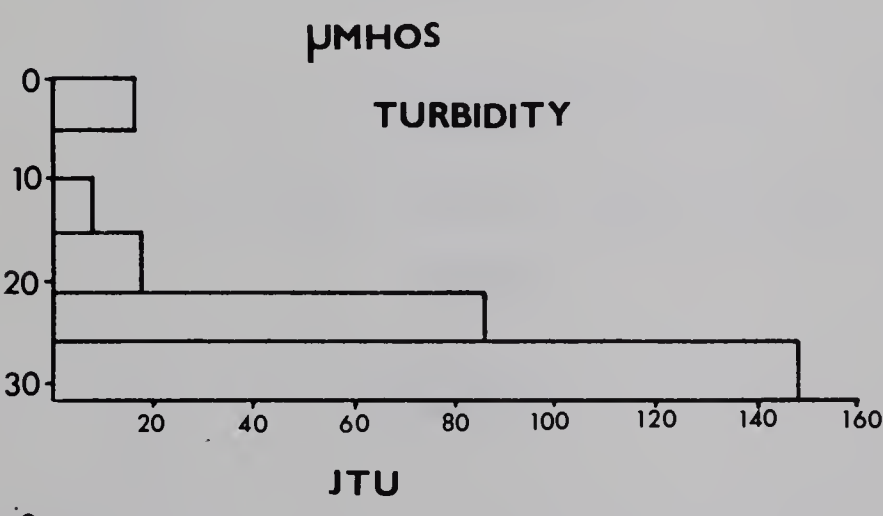
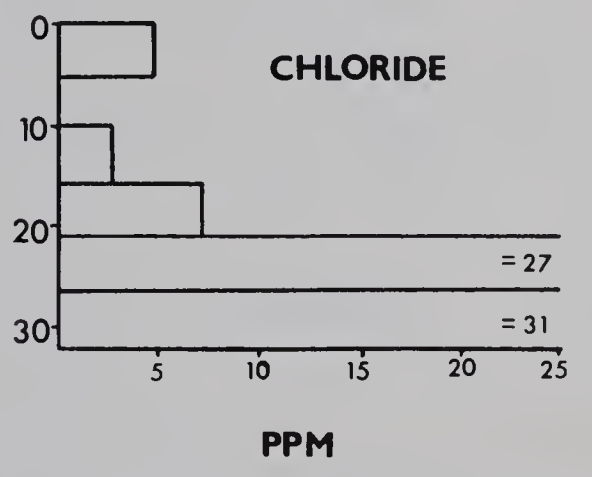
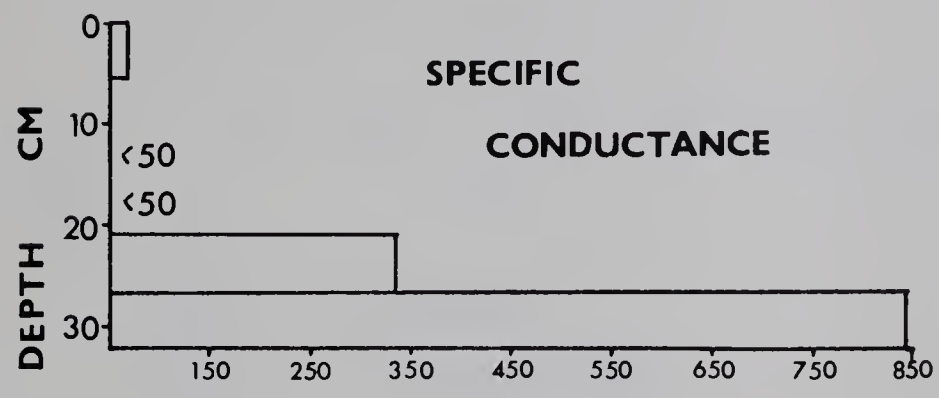
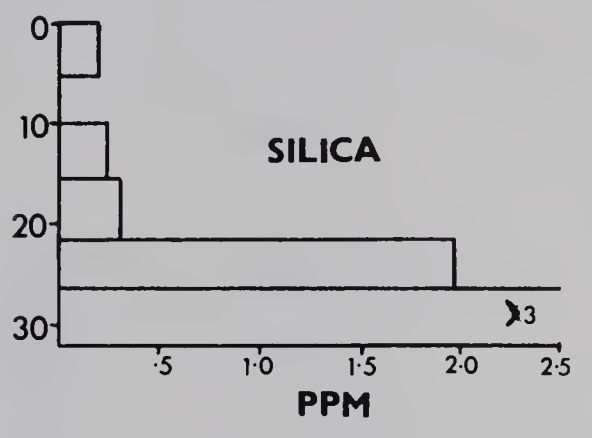
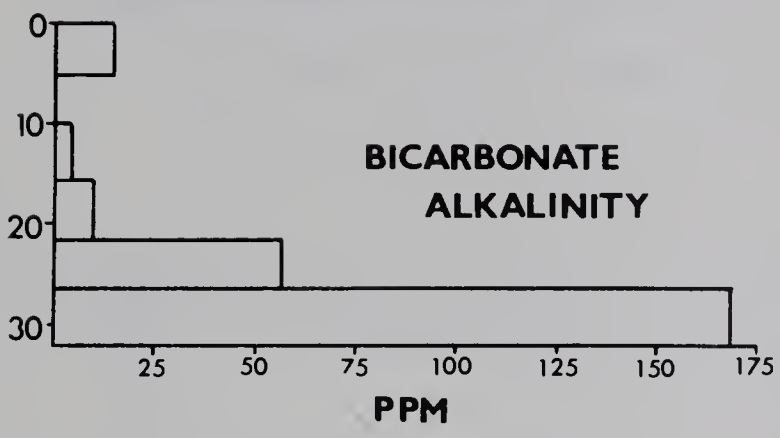
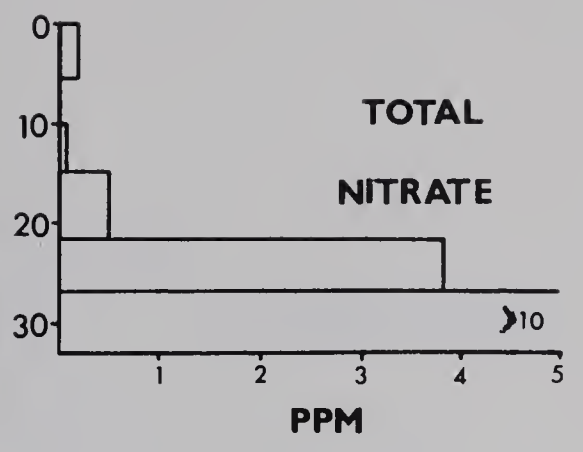
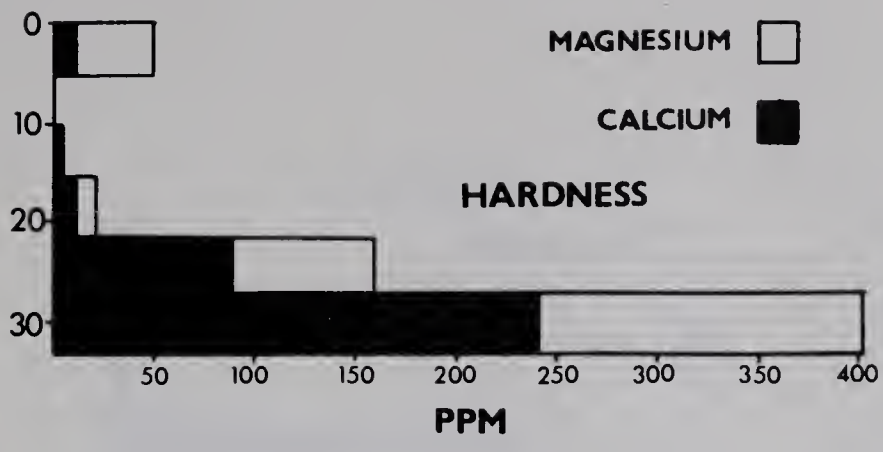


Figure 10. *Variation in physical and chemical characteristics
of ice, December 30, 1967*

JTU Jackson Turbidity Units

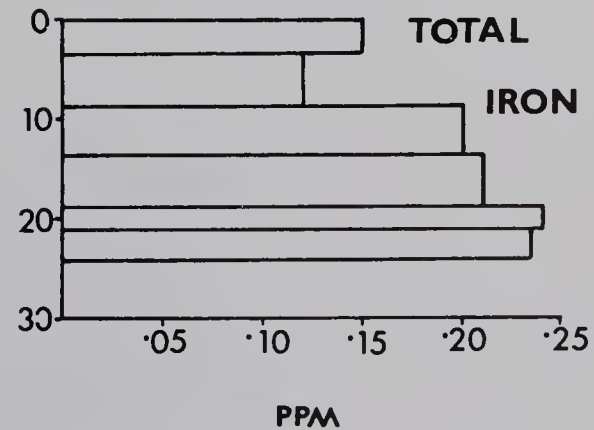
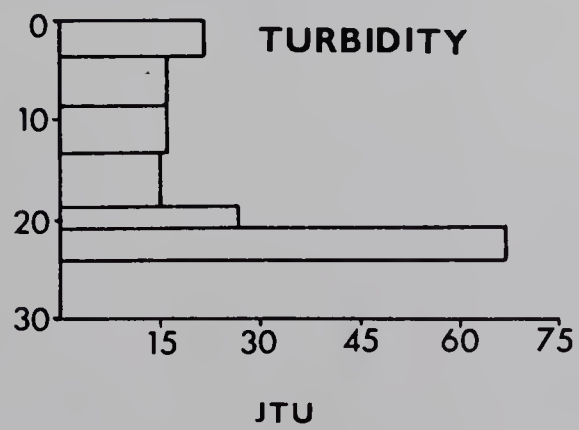
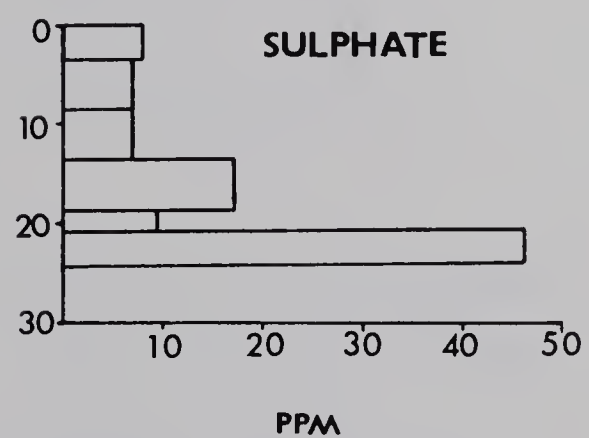
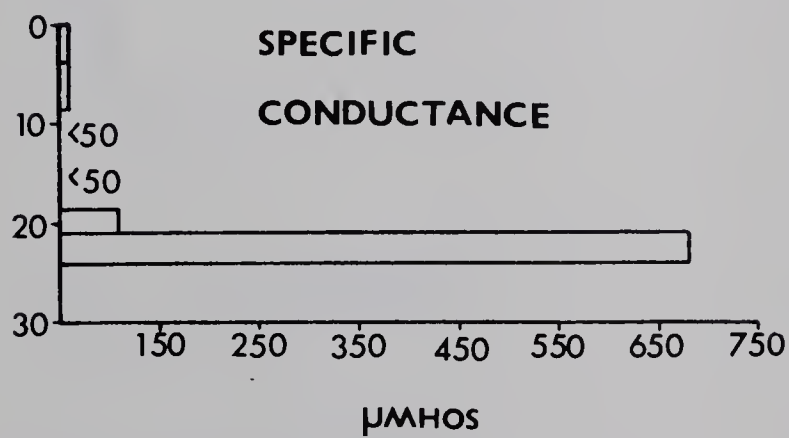
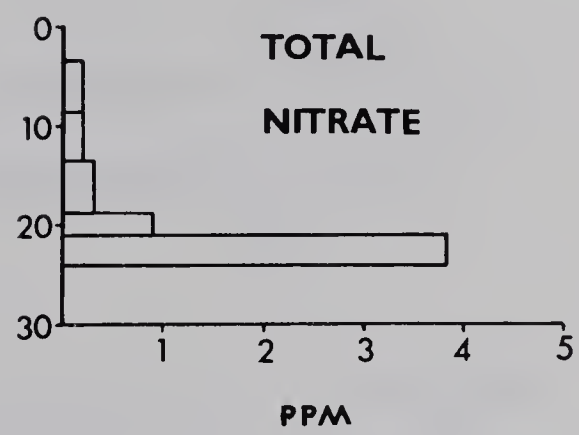
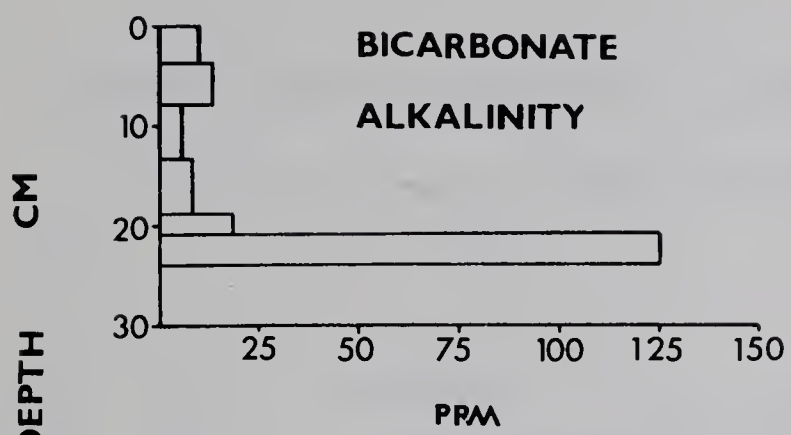
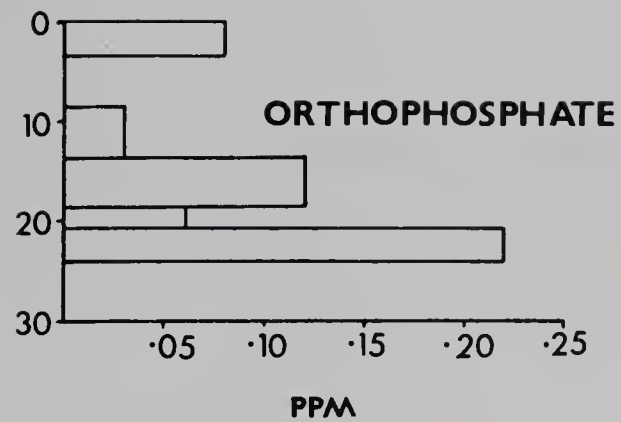
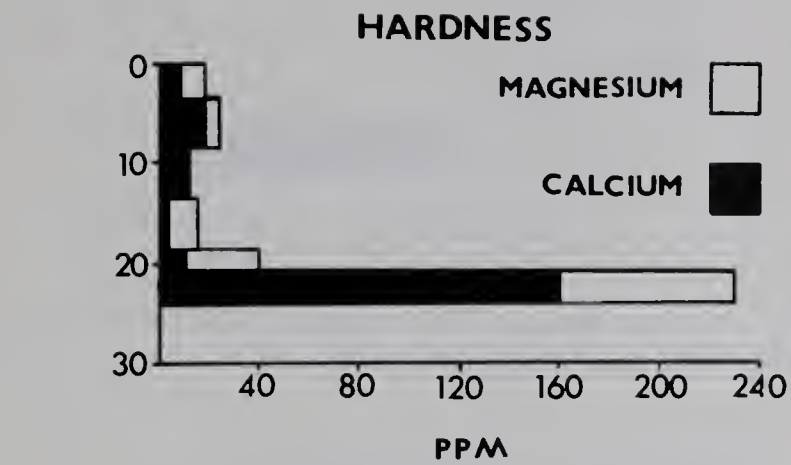


Figure 11. *Variation in physical and chemical characteristics
of ice, December 30, 1967*

JTU Jackson Turbidity Units

Figure 12. *Variation in physical and chemical characteristics
of ice, December 30, 1967*

JTU Jackson Turbidity Units

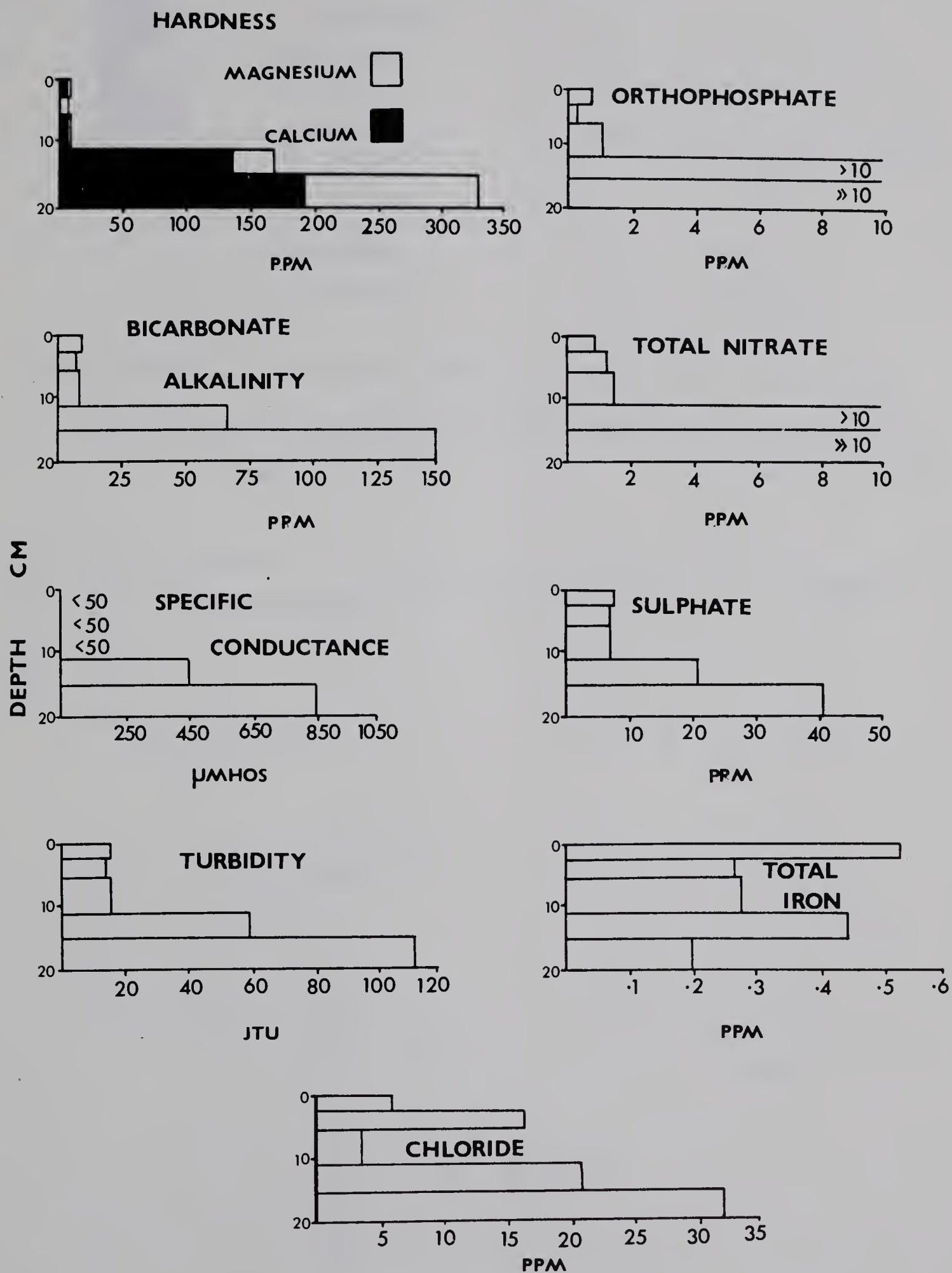


Figure 13. *Variation in physical and chemical characteristics
of ice, January 30, 1968*

JTU Jackson Turbidity Units

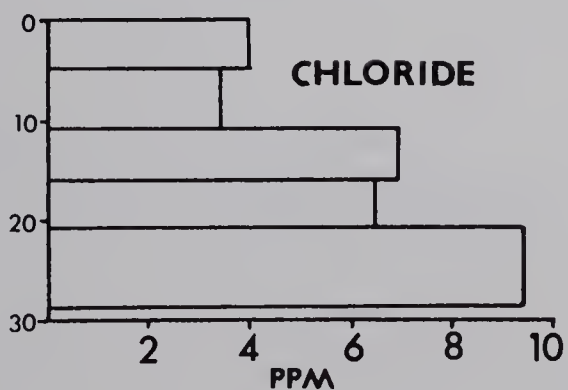
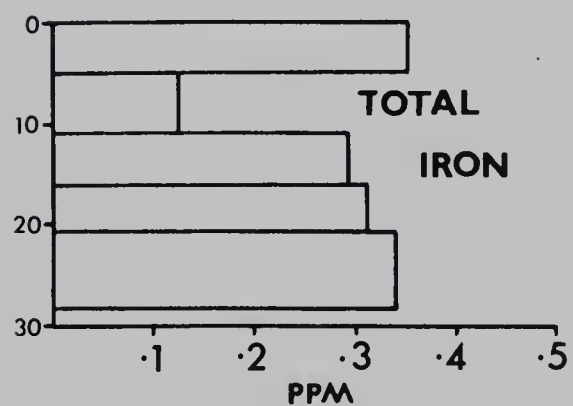
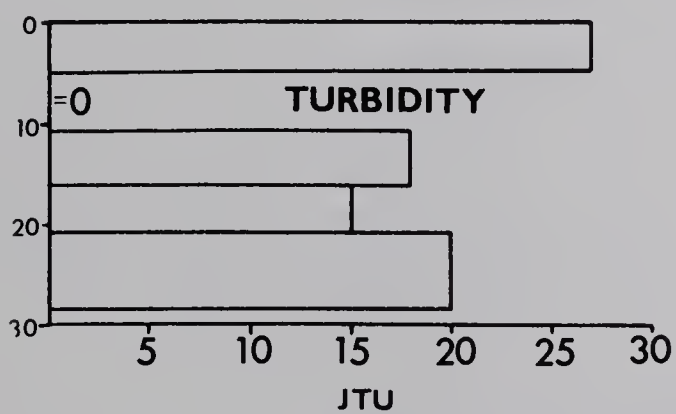
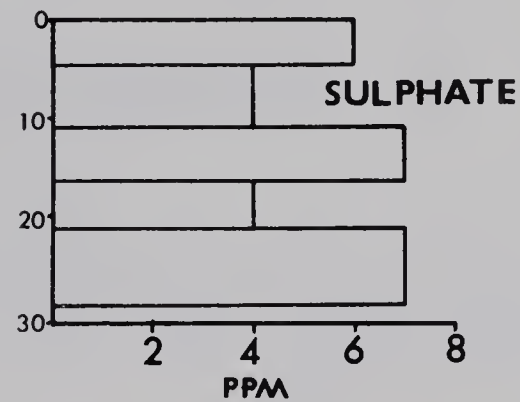
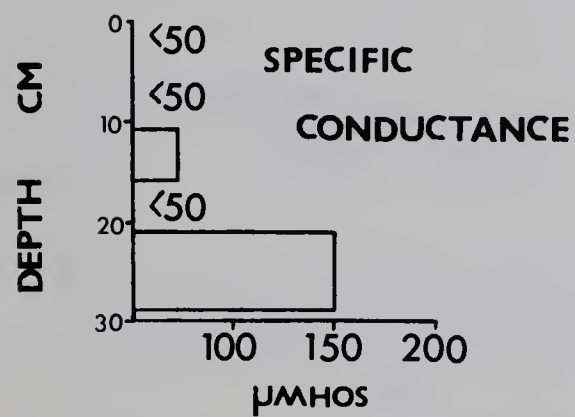
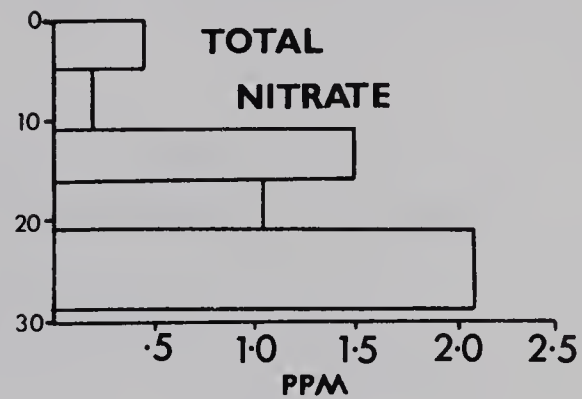
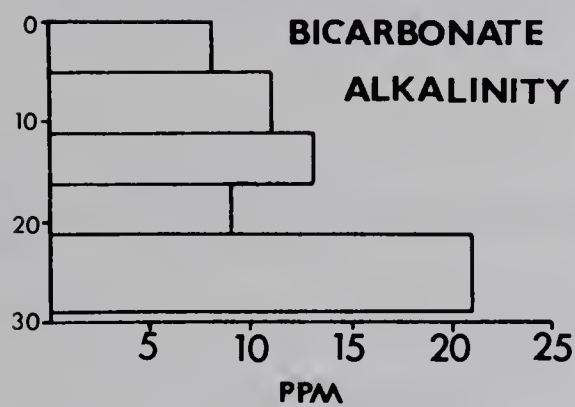
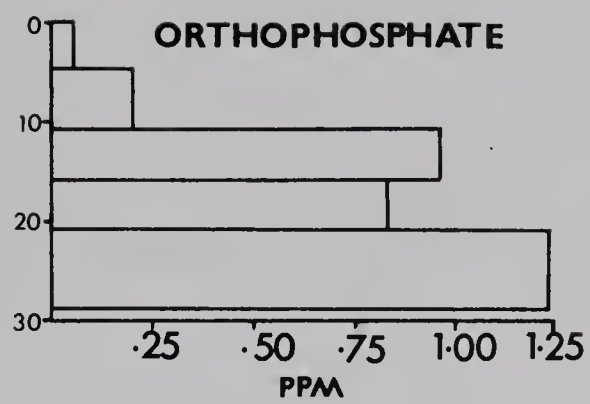
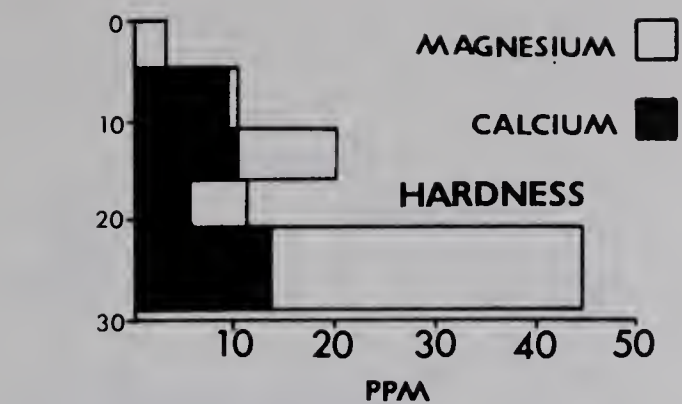
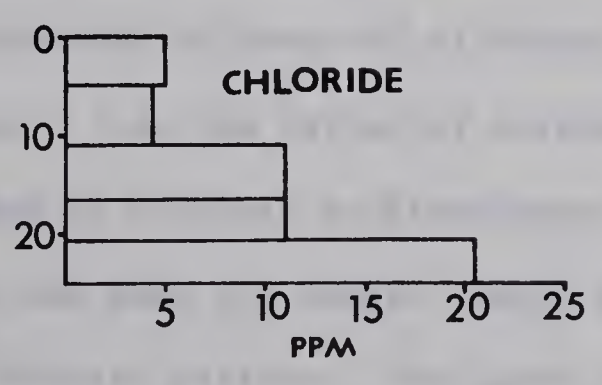
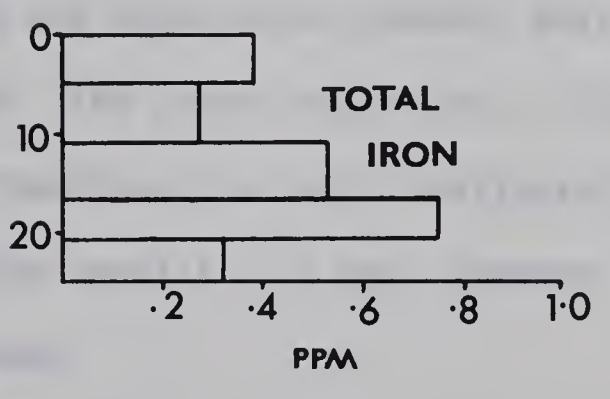
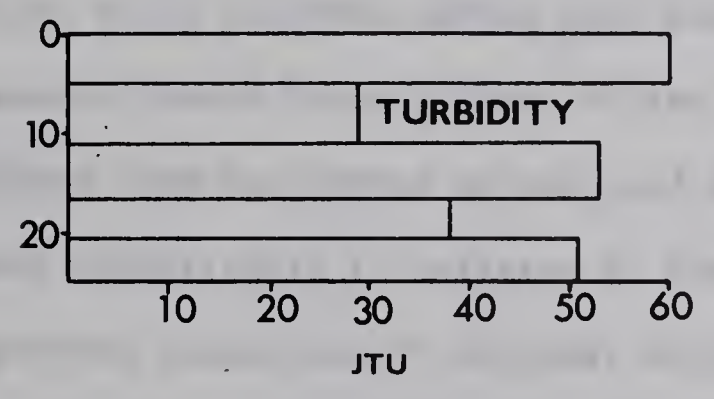
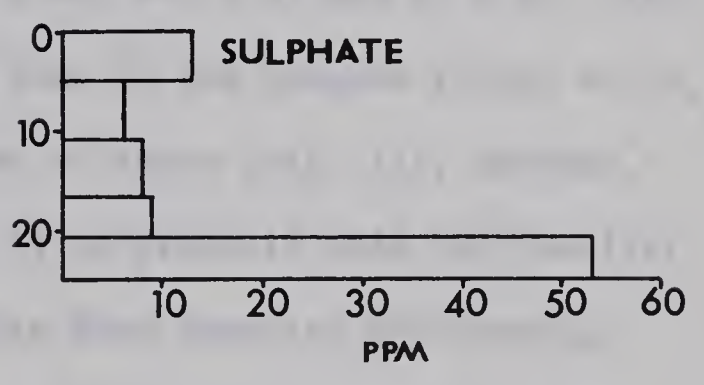
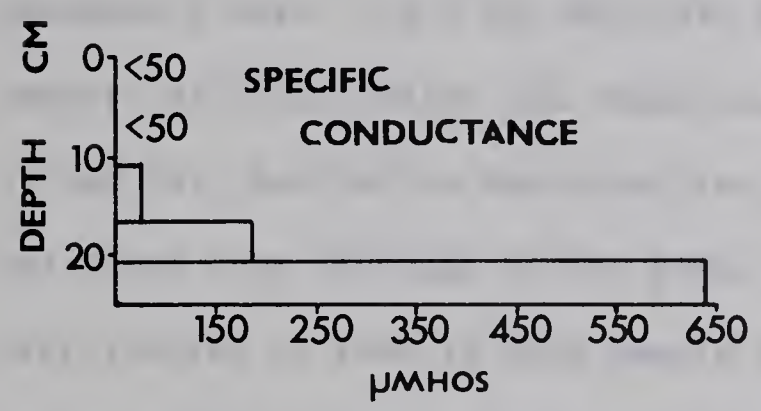
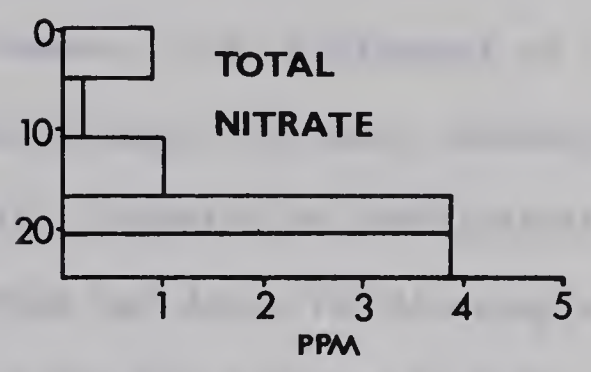
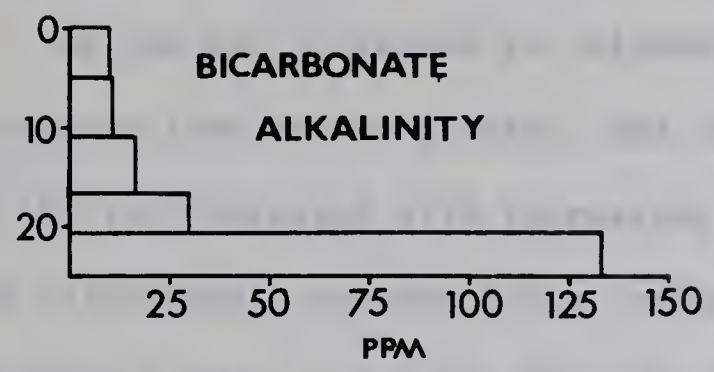
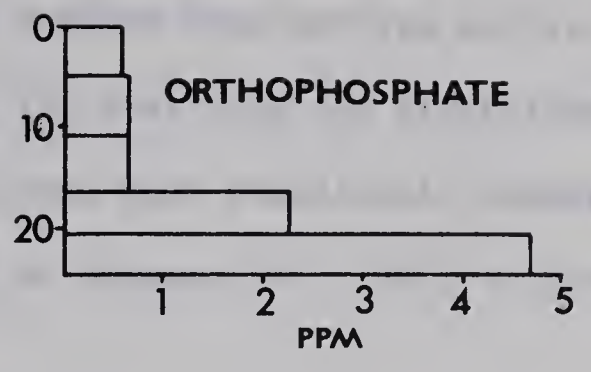
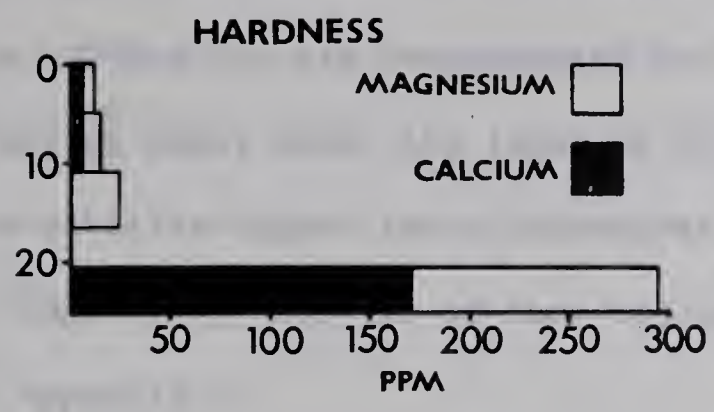


Figure 14. *Variation in physical and chemical characteristics
of ice, January 30, 1968*

JTU Jackson Turbidity Units



above, with the result that the first-formed ice contained only a small percentage of the ions in the water. Secondly, the results obtained for the surface ice are contaminated by ions derived from melting and re-freezing snow; thus, the layer of cloudy ice overlying the first-formed ice exhibits higher ionic concentrations than that immediately beneath. A comparative analysis of snow collected on December 30, 1967, is given in Appendix V.

As the ice increased in thickness, however, the involvement of inorganic ions became greater, and correspondingly the ionic concentration of the ice increased with increasing depth. Correlation coefficients for the relationship between ionic concentration and depth for the sample on December 9 were : Ca 0.92; Mg 0.94; HCO_3 0.90; PO_4 0.97 and Cl 0.96. This pattern of distribution was exhibited by four of the samples (Figs. 9, 10, 12 and 14), but not by the other two. One of these (Fig. 11), however, was taken from the edge of the pond, and it is probable that the peculiar distribution of ions in this sample results from freezing and thawing cycles which occurred during this winter, and which were probably more frequent toward the periphery of the pond. The other sample (Fig. 13) was derived from the centre of the pond and therefore its ionic configuration seems inexplicable in relation to the other results. It may, however, be a further indication of regional differences.

There is some additional evidence of differential treatment of ions in the freezing process : i.e. the ratios of calcium to magnesium, of sulphate to chloride and of sulphate to bicarbonate varied considerably at different levels in the same ice sample (Table 8). These variations seem to conform to a diphasic pattern: the upper 10-15 cm of ice exhibited a progressive increase in both the Ca:Mg and SO_4 :Cl ratios; below this

Table 8. Variation in selected ionic ratios with depth in the ice

Date	Figure	Ratio	Approximate Depth (cm)					
			0-5	5-10	10-15	15-20	20-25	25-30
<u>1967</u>								
Dec. 9	9	Ca:Mg	0.3	-	2.0	1.0	1.2	1.5
		SO ₄ :Cl	0.8	-	1.0	0.4	0.6	-
		SO ₄ :HCO ₃	0.2	-	0.8	0.4	0.3	-
Dec. 30	10	Ca:Mg	0.8	3.0	5.0	0.3	0.4	2.3
		SO ₄ :HCO ₃	0.8	0.5	1.2	1.9	0.5	0.4
	11	Ca:Mg	4.0	0.0	0.0	0.3	-	-
		SO ₄ :Cl	1.0	1.5	0.7	1.0	-	-
		SO ₄ :HCO ₃	0.3	0.3	0.4	0.3	-	-
	12	Ca:Mg	0.4	1.3	3.4	1.4	-	-
		SO ₄ :Cl	0.9	2.0	1.0	1.3	-	-
		SO ₄ :HCO ₃	0.8	0.9	0.3	0.3	-	-
<u>1968</u>								
Jan. 30	13	Ca:Mg	0.0	9.0	1.0	0.8	0.6	-
		SO ₄ :Cl	1.5	1.1	1.0	0.6	0.7	-
		SO ₄ :HCO ₃	0.8	0.4	0.5	0.4	0.3	-
Jan. 30	14	Ca:Mg	1.3	0.7	-	0.0	1.4	-
		SO ₄ :Cl	2.6	1.3	0.7	0.8	2.5	-
		SO ₄ :HCO ₃	1.4	0.6	0.5	0.3	0.4	-

level, a second increase occurred. This depth would seem to correspond to the depth of ice (8 cm) which persisted for three weeks in early November and was subsequently followed by rapid ice growth. In contrast, the ratio of sulphate to bicarbonate concentration seems to fluctuate irregularly.

Selective involvement of ions has been demonstrated with respect to sea ice. Thus Wiese (1930) and Arnol'd-Aliab'ev (1933) have shown that the $\text{SO}_4:\text{Cl}$ ratio increases with depth in the ice, and Arnol'd-Aliab'ev (1933) demonstrated a similar change in the $\text{CO}_3:\text{HCO}_3$ ratio. The reasons for this phenomenon are as yet obscure, but Bennington (1967) has reported that the salinity of sea ice may vary by as much as two or three per cent at two points at the same depth and a few inches apart. He attributes this to random inclusion of sea water trapped by the formation of new ice platelets beneath an existing ice sheet.

The diphasic pattern reported here, however, may be the result, in part at least, of the ageing of the ice. This phenomenon is well-documented in sea ice (Malmgren, 1927; Chernigovskii, 1939): it is apparently the result of migration of the enclosed salts through the ice by freezing and thawing cycles initiated in the presence of a temperature gradient (Sverdrup, 1926; Schulz, 1930; Pounder, 1965). With respect to sea ice, however, measurable decreases in salinity take several weeks to occur in this manner (Dzens-Litovskii, 1954). An alternative, or perhaps concomitant influence may be the rate of freezing. Arnol'd-Aliab'ev (1933) has demonstrated that the salinity of sea ice is increased by more rapid freezing, but more extensive data would be required to analyse the present results from this point of view.

From an ecological viewpoint, the profound changes resulting from

total freezing in winter are difficult to assess. It is clear, however, that for at least two months a period of relative dormancy must occur, which represents a particularly interesting and probably significant parameter of the environment. It is difficult at the present stage to imagine the effects on the biological community of the changing ionic concentration associated with freezing.

BIOLOGICAL CHARACTERISTICS

Throughout the study, major emphasis has been laid on the faunal community, with particular respect to its seasonal changes in composition and abundance. Changes in community composition from 1967 to 1968 were very extensive, presumably as a result of the striking alterations in physical (and perhaps chemical) parameters of the environment.

1. Macrophytes

The dominant terrestrial and semi-terrestrial macrophytes surrounding and invading the pond have been outlined above (P.4). Of the semi-terrestrial flora, beaked sedge (*Carex rostrata* Stokes) and tall manna grass (*Glyceria grandis* S.Wats.) were most abundant in 1967, forming a distinct band around the pond which varied in width from 5 m (north and west edges) to 20 m (east and south edges). Both species are common in wet places surrounding ponds and 'sloughs' of the aspen parkland (Bird, 1961; Budd and Best, 1964). In the same year, the creeping spike rush, *Eleocharis palustris* (L), occurred in rather less abundance than the other two. Occasional patches of long-stalked chickweed (*Cerastium nutans* Raf.), and small yellow water-crowfoot (*Ranunculus gmelinii* DC.) were also present.

In 1968, however, the emergent community was quite different from the previous year. In greatest abundance was *Eleocharis palustris*, with *Glyceria grandis* in approximately the same density as in 1967; the occurrence of *Carex rostrata* was restricted in this year to a series of isolated patches, particularly on the north and west edges, where the recession of water, and accordingly the environmental change, appeared to be less extensive. This striking change in abundance was undoubtedly a function of the low water level, which presumably provided a more suitable habitat for *Eleocharis* than for *Carex*. The floral ecology of temporary and

permanent ponds is imperfectly known, however (Lippert and Jameson, 1964), and it is therefore impossible to relate these changes in flora to specific environmental changes.

The truly aquatic (*sensu stricto*) macroflora was restricted to three species in 1967: lesser duckweed (*Lemna minor* L.), ivy-leaved duckweed (*Lemna trisulca* L.) and the spiked water milfoil (*Myriophyllum exalbescens* Fern.). *Lemna minor* was abundant in 1967, but as a result of wind action was restricted entirely to the west and southwest edges of the pond. In 1968 it was very scarce. The exposure of the pond to northerly and northeasterly winds is an extremely important ecological factor : the restriction of *L. minor* to one end prevents its development over the whole surface of the water, and hence limits the effect of shading.

Of the other two species, both of which are submerged plants, *L. trisulca* was by far the most abundant. Both, however, had an uneven distribution in the pond, being far more dense at the eastern and southern edges than elsewhere. This distribution is also clearly a function of wind action and the loose sediment forming the bottom of the pond. No attempt was made to investigate the ecological effects of these species, but Buscemi (1958) has shown that a plant with similar growth form (*Elodea canadensis* Michx.) may cause severe local oxygen depletion when abundant. In 1968 both aquatic species were present, but growth was apparently very poor.

It is clear that changes in the macrophyte section of the community, both seasonal and between years, represent significant features of the environment. It is not possible, however, to correlate these changes more closely with either changes in physico-chemical features, or changes in fauna.

2. Phytoplankton

Data concerning the seasonal abundance and occurrence of phytoplankton were seriously limited by the method of examination and the unfortunate loss of two samples. As a result of the large scale changes that took place between one year and the next, it is not really feasible to make any distinction between permanent and adventitious species.

Four species occurred in abundance at one time or another during the study: *Aphanizomenon flos-aquae* (L.), *Anabaena spiroides* Lemm., *Spirogyra* sp. and *Fragilaria* sp. Their relative abundance during the months for which samples were retained is shown in Figure 15, together with an approximation of the total number of cells per litre at that time. In the summer of 1967 (June) *Aphanizomenon* occurred in bloom proportions, and constituted almost 100% of the association at that time. Hammer (1964) has demonstrated that blooms of this particular species are prevalent at temperatures in the range 22.5°C to 26.5°C. As mentioned above, it apparently ceased abruptly between July 16 and 19, and thereafter the total phytoplankton association amounted to less than 2% of the concentration in June. Although *A. flos-aquae* was still the most abundant species in September, it was succeeded in October by the pennate diatom *Fragilaria* sp. which remained dominant throughout the winter and into the spring of 1968. During May, 1968, *Spirogyra* sp. and *Anabaena* sp. occurred in addition to *Fragilaria*.

3. Zooplankton

Several genera of rotifers have been provisionally identified from the pond in both years (Appendix I). Considering the ease with which they may be transported, however, (Hutchinson, 1967) the distinction between adventitious and permanent members of the community is meaningless in this situation. Four species, *Keratella cochlearis* (Gosse), *K. quadrata* (Müller),

Figure 15. *Relative abundance of major phytoplankton species,
1967 and 1968*

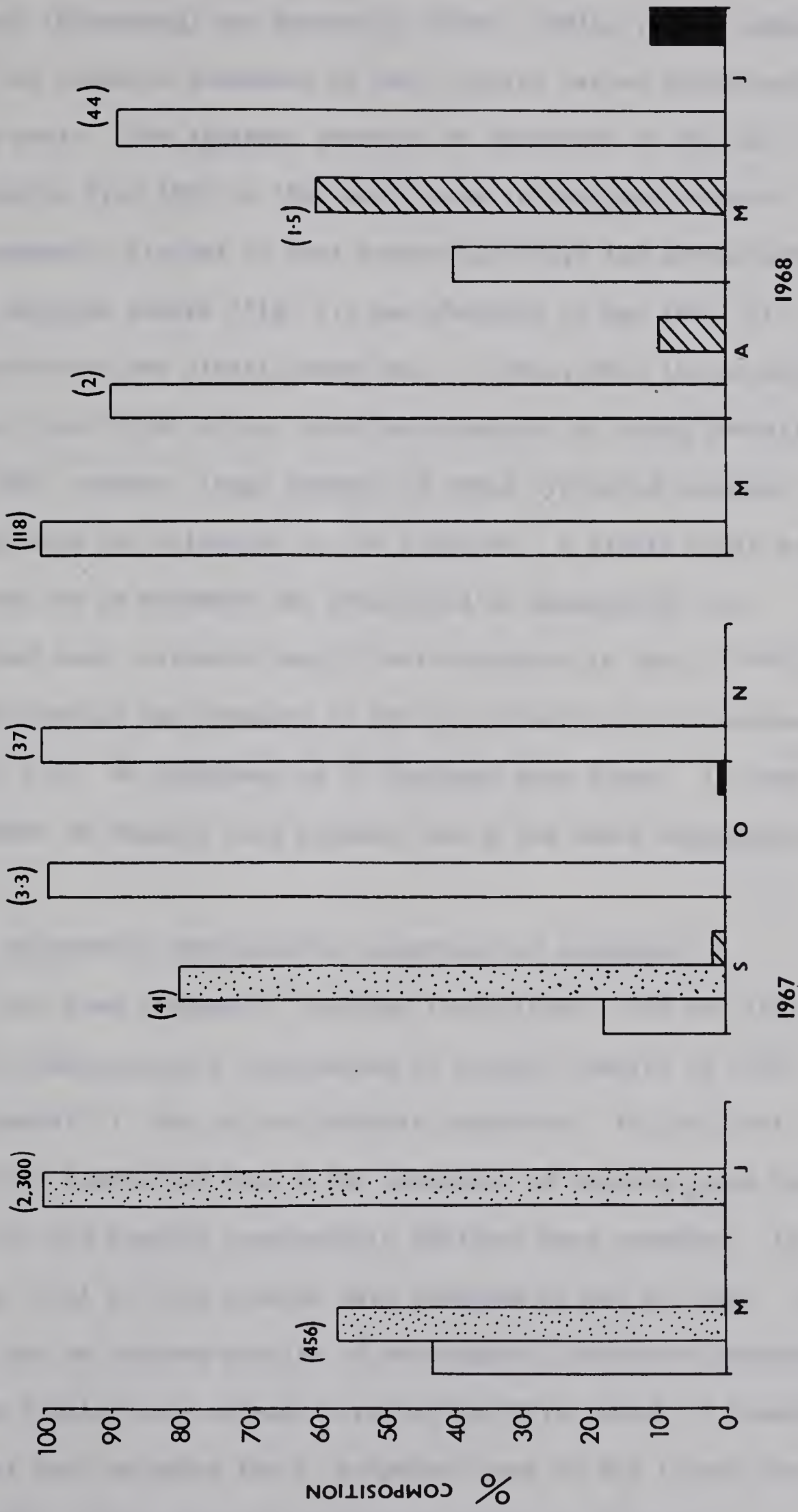
() Abundance in cells per litre $\times 10^6$

FRAGILARIA SP.

APHANIZOMENON FLOS-AQUAE

SPIROGYRA SP.

ANABAENA SPIROIDES



Filinia longiseta (Ehrenberg) and *Monostyla lunaris* (Müller) were common (Fig. 16), but the relative abundance of each species varied considerably between the two years. The apparent reversal of dominance of the two species of *Keratella* from 1967 to 1968 would seem to indicate a major change in the community similar to that occurring within the phytoplankton.

Diaptomus leptopus Forbes (Fig. 17) was abundant in May 1967, at which time reproduction was clearly under way: in June, when the population had reached more than 90 per litre, 69.4% were nauplii or young juveniles. By September, 1967, however, large numbers of young cyclopoid copepods had entirely replaced the calanoids in the plankton. A single adult male obtained from the ice in November was identified as *Mesocyclops* sp.

In the second year, calanoid nauplii were abundant in April (790/litre), but the adults occurring and breeding in May were *Diaptomus franciscanus* Lilljeborg (Fig. 17). No specimens of *D. leptopus* were found. In June 1968, large numbers of nauplii were present, and a few adult *Mesocyclops* sp.

Unlike the apparently monospecific occurrence of calanoids, a phenomenon that has been frequently recorded (Hutchinson, 1965 and 1967; Cole, 1967), the Cladocera were represented by several species in 1968 (Fig. 17 and Appendix 1), and in considerable abundance. In the first year, the group was scarce and only a few specimens of *Daphnia pulex* Leydig, *Daphnia rosea* Sars and *Bosmina longirostris* (Müller) were recorded. In 1968, however, a total of nine species were obtained in May and June. Of these, *D. pulex* and an unknown species of *Moinodaphnia* were most abundant. In May, *D. pulex* females were already carrying ephippia, which is somewhat earlier than that date recorded for *D. schødleri* Sars in Big Island Lake, Alberta (Lei, 1968). Four species, *Polyphemus pediculus* (Linné),

Figure 16. *Seasonal abundance of major species of Rotifera,
1967 and 1968.*

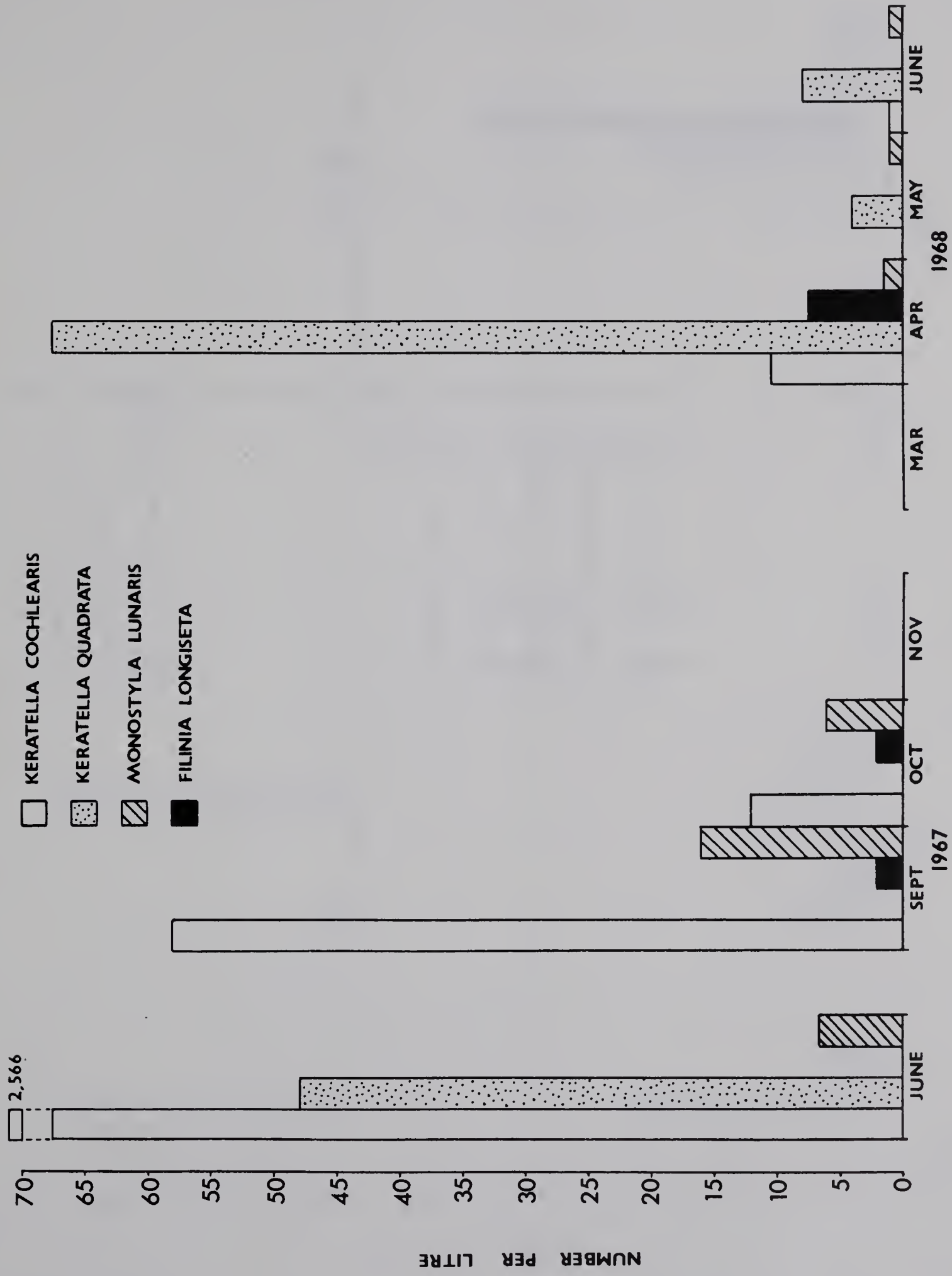
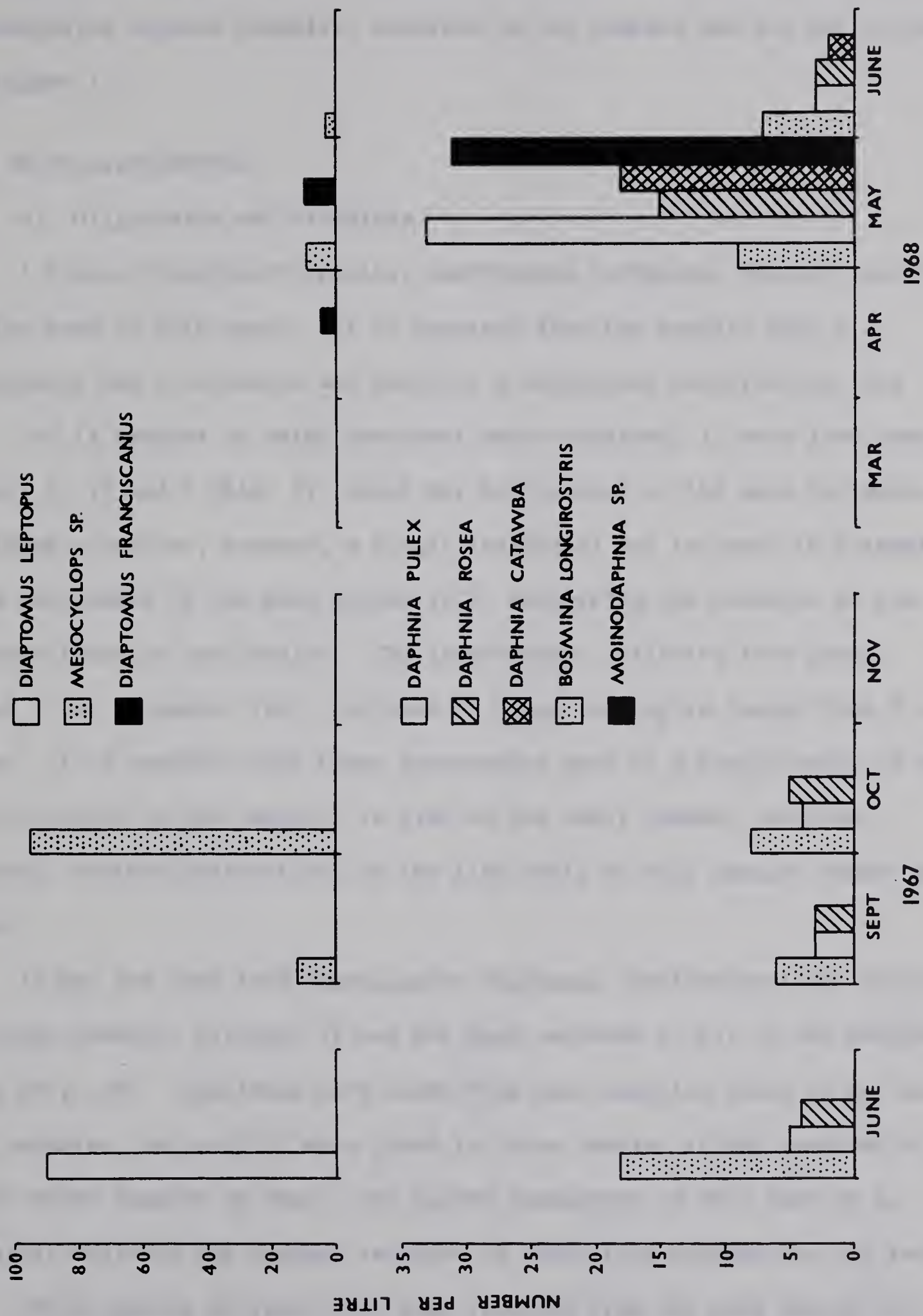


Figure 17. *Seasonal abundance of major species of Copepoda and Cladocera, 1967 and 1968.*

Upper : Copepoda

Lower : Cladocera





Scapholeberis kingi Sars, *Graptoleberis testudinaria* (Fischer), and *Simocephalus vetulus* Schødler, occurred in low numbers and are not included in Figure 17.

4. Macroinvertebrates

a) Oligochaeta and Hirudinea

A single oligochaete species, *Lumbriculus variegatus* (Müller) was found in the pond in both years. It is apparent from the results that *L. variegatus* had a nonrandom and possibly a contagious distribution (Fig. 18) : of 14 samples in which specimens were contained, 11 were from sample points I, II and V (Fig. 2), which may be regarded as the more peripheral. On three occasions, however, a single individual was included in a sample from the centre of the pond (point III), indicating the presence of the species there at low density. The large number collected from sample point II in September 1967, included 32 young ranging in length from 3 to 5 mm. It is probable that these represented part of a single batch of eggs which hatched in that month. In view of the small numbers involved, however, further observations on the life cycle of this species cannot be made.

In May and June 1968 *Chaetogaster diaphanus* (Gruithuisen) was obtained in large numbers, although it had not been recorded at all in the previous year (Fig. 18). Specimens were taken from each sampling point on at least one occasion, but only 21 were found in three samples in May compared with 58 in three samples in June. The sudden appearance of this species in quantity reflects the changes recorded in other taxa between the two years.

Three species of leech have been recorded from the pond during the course of the study: *Oculobdella lucida* Meyer and Moore; *Glossiphonia heteroclita* (L.) and *Helobdella fusca* (Castle). Specimens of *O. lucida*

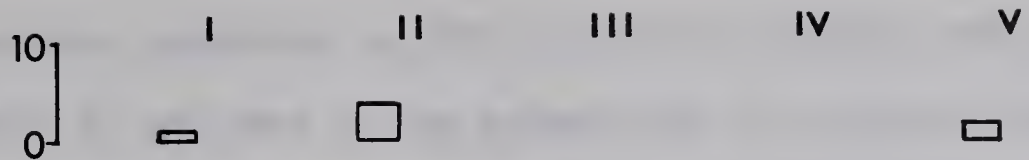
Figure 18. *Number of Lumbriculus variegatus and Chaetogaster diaphanus in vertical samples, 1967 and 1968*

Open blocks : *Lumbriculus variegatus*

Closed blocks : *Chaetogaster diaphanus*

I - V : Sample points

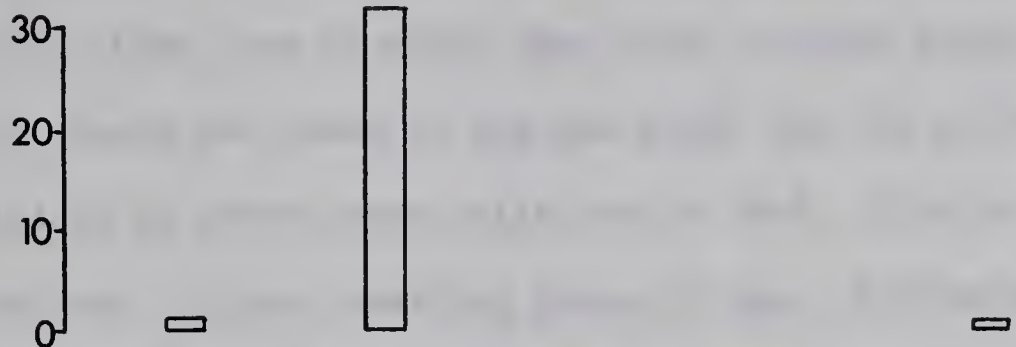
1967
JULY



AUG



SEPT



OCT



NOV

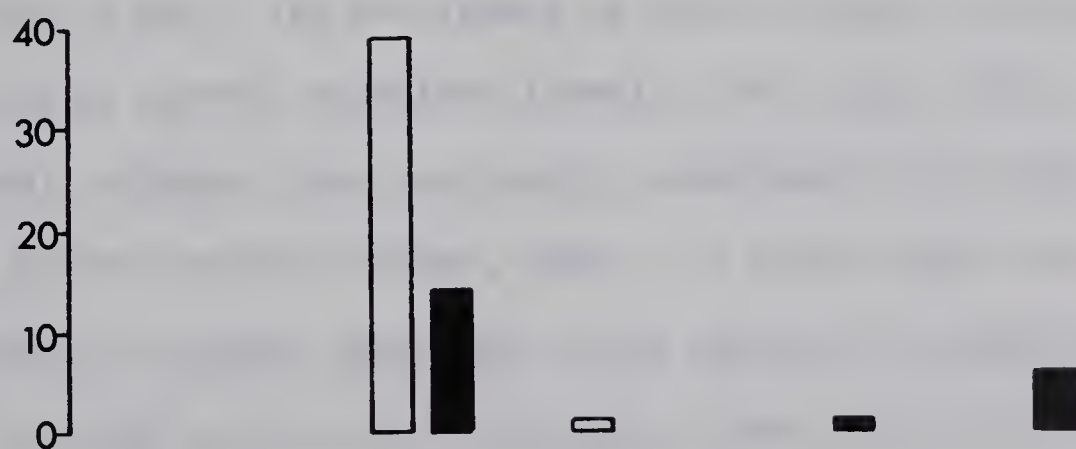


1968

APR



MAY



JUNE



were obtained on several occasions in 1967 in vertical samples and general collections (Appendix I) and once in the second year in a dip net (April 26). None of these specimens carried eggs, although Moore (1964) reported that the breeding period for this species lasts from June through September in permanent ponds in Alberta. Seven individuals of *G. heteroclita* were taken during the study, one of which (May 1968) carried young. The first specimen of *H. fusca* was found in the mud below the ice on December 9, 1967, but a total of 16 others were collected in 1968. Five of these, taken on May 29 and June 15, were carrying young or eggs, indicating a reproductive period earlier than that recorded by Moore (1966). This may be a reflection of the early spring in 1968.

b) Anostraca and Conchostraca

In early April 1968, large numbers of the phyllopod *Eubbranchipus* (=Chirocephalopsis) *bundyi* were seen in the pond. Four specimens taken by dip net on April 19 included two mature females carrying eggs in the ovisac, and other adults were observed one week later. None were seen, however, after the first week in May. The occurrence of fairy shrimps in permanent ponds has been noted on several occasions (Jewell, 1927; Kenk, 1949; Hartland-Rowe, 1966), although they are usually considered to be more characteristic of astatic waters (Mozley, 1932). It would appear that the success of this group is largely dependent on the absence of predators for at least part of the life cycle, and an extensive summer recession of water from parts of the pond basin where the eggs may be dried. With respect to the first requirement, the persistence of ice at the bottom of the pond through part of April was probably important, since many potential predators would thereby have been absent for the early growing period.

On May 31, 1967, a large number of small *Lynceus mucronatus* were

obtained by dip net: at this time they constituted 32.6% of the total macro-invertebrate association. The species was not recorded again in that year. Metanauplii were taken in plankton samples on April 26, 1968, at a density of 18/litre, and subsequently, dip net samples were obtained in order to establish the life cycle of the population (Fig. 19). A single specimen in the process of transformation from the metanauplius to the adult was caught on June 19. Its maximum length was 1.26 mm, which corresponds with the smallest adults captured (Fig. 19). Growth of the adults from a length of 1.25 mm at transformation to the maximum of 3.5 - 4.0 mm appears to take 3 - 4 weeks.

It is apparent that hatching may occur over an extended period of time, in this instance, from late April through May 1968. Vertical samples taken in May and June (Table 9) indicate a tendency toward greater density in the centre of the pond.

c) Ostracoda and Amphipoda

When the pond was first visited on February 5, 1967, fragments of ice were collected and allowed to thaw in an aquarium. A large population of ostracods (*Candona* sp. and *Cyclocypris ampla* Furtos), three coenagrionid nymphs and a single specimen of *Hyalella azteca* (Saussure) were obtained alive from the melt.

No ostracods were included in samples taken during the summer of 1967; *Candona* sp., however, appeared in September and October at an average density in each case of 680/m² (Fig. 20). All specimens found in ice samples collected for chemical analysis during the winter of 1967-68 were kept and counted, and from these data the average density was calculated as 691.2/m². Most of the specimens from the ice seemed to survive, despite the artificial conditions of thawing, and it is assumed on this

Figure 19. *Population length-frequency histogram for*
Lynceus mucronatus adults, 1968

() indicates number of individuals captured



MAY 17
(195)



MAY 21
(108)



MAY 25
(139)



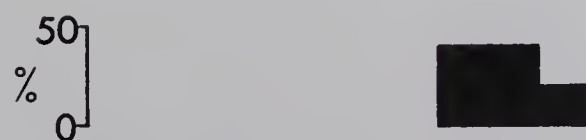
MAY 29
(155)



JUNE 6
(33)



JUNE 15
(48)



JUNE 24
(5)

1.0 1.5 2.0 2.5 3.0 3.5 4.0 4.5 5.0

MAXIMUM LENGTH

(mm.)

Table 9. *Number of Lynceus mucronatus in vertical samples, May and June, 1968*

	Sample Point				
	I	II	III	IV	V
May	1	-	1	99	2
June	2	-	6	2	3

Figure 20. *Abundance of Candona sp., Cyclocypris ampla and
Cypris sp., 1967 and 1968*

-I - V Sample points

1967 I II III IV V

SEPT

50
0

OCT

50
0

1968

APR

NUMBER / VERTICAL SAMPLE

50
0

MAY

100
50
0

JUNE

50
0



CANDONA SP.



CYCLOCYPRIS AMPLA



CYPRIS SP.



basis that a large population remains alive at the end of winter. In April and May, 1968, *Candona* sp. was abundant, but no specimens were taken in June.

Cyclocypris ampla also appeared in September 1967 and again in 1968 (April) at an apparent density of 190/m². It was encountered occasionally in ice samples during the winter, but clearly in lower abundance than *Candona* sp.

A third species, *Cypris* sp. was collected for the first time in May 1968 (Fig. 20), when it appeared to be present in large numbers: four samples in which it occurred gave an average density of 4,058/m². In June, however, only a single specimen was obtained.

When field work began in May 1967, it was noted that the bottom sediments in the centre of the pond were littered with the remains of dead amphipods. In order to establish the presence or absence of amphipods an intensive sampling programme was instituted using a square net (11.8 meshes/cm) with an area of 0.47m². This was towed behind the boat for distances of 5 or 20 m (May 29 and 31, 1967). A single, live individual of *Gammarus lacustris* Sars was obtained. Occasional observations of *G. lacustris* or *H. azteca* were made in 1967 and 1968, but no measurable population occurred at any time during the study.

It was considered possible that the few specimens seen in the two years were immigrants. In order to test this, 12 ducks of several species were shot and the plumage examined for invertebrates. Although in one instance, a male green-winged teal (*Anas carolinensis*) collected near Azure Lake, Alberta, carried six small (3-5 mm) *H. azteca*, the probability of transport in this manner is low, but it is equally obvious that such dispersal will occur as waterfowl move between feeding and roosting

grounds.

The failure of this group to establish a persistent population in the pond may be attributed to several factors. Dineen (1953), for example, has reported that *H. azteca* is sensitive to high summer temperatures (i.e., above 25°C). The single, viable specimen of *H. azteca* obtained from the ice block indicates that freezing is not necessarily lethal, but presumably may augment an already high death rate during the winter (Menon, 1966).

d) Odonata and Ephemeroptera

Three species of Zygoptera (Coenagrionidae) formed a conspicuous section of the community in 1967. Specific identification of the nymphs was impossible in many cases, but 1967 emergence trap results indicated that the relative numbers of the three species *Coenagrion angulatum* Walker, *C. resolutum* (Hagen) and *Enallagma boreale* Selys were 14:3:1 respectively. Vertical samples (Fig. 21) showed an average density of over 200 nymphs/m² but since more than half of the samples did not contain a single specimen, it is probable that a clumped distribution applied.

Emergence patterns for these three species are shown in Figure 22. *C. angulatum* was first recorded on June 2, 1967, but most tenerals were trapped between June 13 and 29. The low numbers obtained between June 20 and 24, 1967 for both species of *Coenagrion* were clearly related to the low temperatures prevailing at this time. The flight period recorded here is almost identical to that given by Walker (1953) in each case.

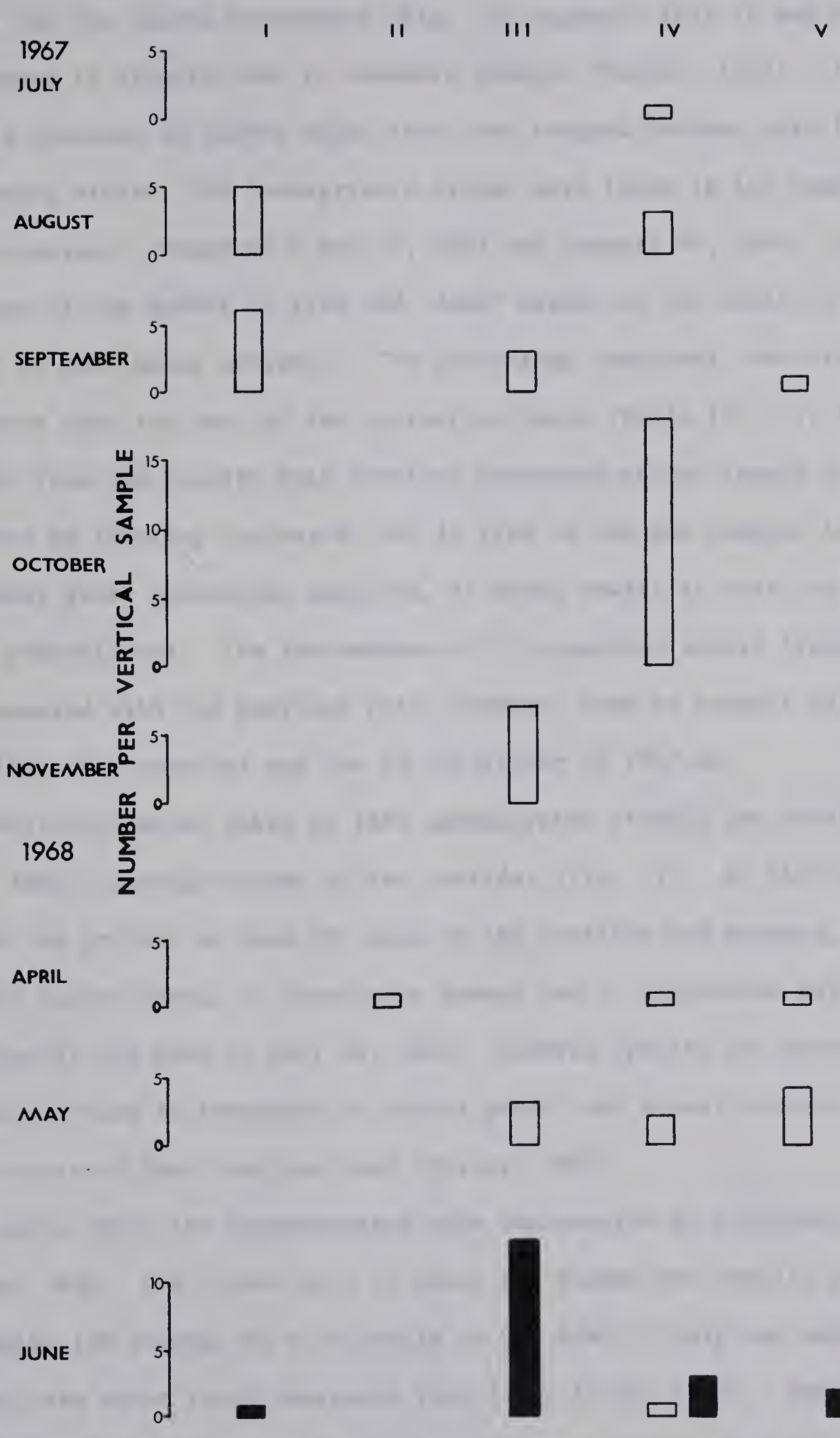
E. boreale tenerals were collected between June 2 and 6, 1967, with a single specimen emerging in the middle of July. Because of the low numbers available there is some doubt as to the extent of the emergence

Figure 21. *Abundance of Zygoptera nymphs in vertical samples,
1967 and 1968*

Open blocks : Coenagrionidae

Closed blocks : Lestidae

I - V Sample points



period, but the second occurrence (Fig. 22) suggests that it may be somewhat longer in Alberta than in southern Ontario (Walker, 1953). In 1967 a single specimen of *Lestes dryas* Kirby was trapped between July 11 and 13.

During winter, 158 coenagrionid nymphs were taken in ice samples on three occasions: December 9 and 30, 1967 and January 30, 1968. Counts were made of the number of live and 'dead' nymphs on the basis of their ability to move about actively. The percentage 'survival' was calculated from these data for each of the collection dates (Table 10). It is apparent from the results that survival decreased as the length of time subjected to freezing increased, but in view of the few samples taken and the rather gross techniques employed, it seems unwise to rely too heavily on the present data. The low numbers of *C. angulatum* adults trapped in 1968 compared with the previous year, however, seem to support the contention that survival was low in the winter of 1967-68.

Vertical samples taken in 1968 demonstrated clearly the replacement of the family Coenagrionidae by the Lestidae (Fig. 21). By the termination of the project on June 28, none of the Lestidae had emerged, but pairs of *Lestes dryas*, *L. forcipatus* Rambur and *L. disjunctus* Selys were collected at the pond on July 18, 1968. Several species of *Lestes* are frequently found in temporary or vernal ponds, and almost certainly have a life-cycle of less than one year (Walker, 1953).

During 1967, the Ephemeroptera were represented by two species, *Caenis simulans* McD. and *Cloeon* sp., of which the former was usually present in samples (an average of 9.35/sample or 908.8/m²). Only one adult *Caenis*, however, was taken in an emergence trap (July 13-16, 1967). During the winter five *C. simulans* and five *Cloeon* sp. were obtained in ice samples, none of which were alive. In the second year no nymphs were collected by

Figure 22. *Emergence patterns of Zygoptera and Chironomidae,*
 1967 and 1968

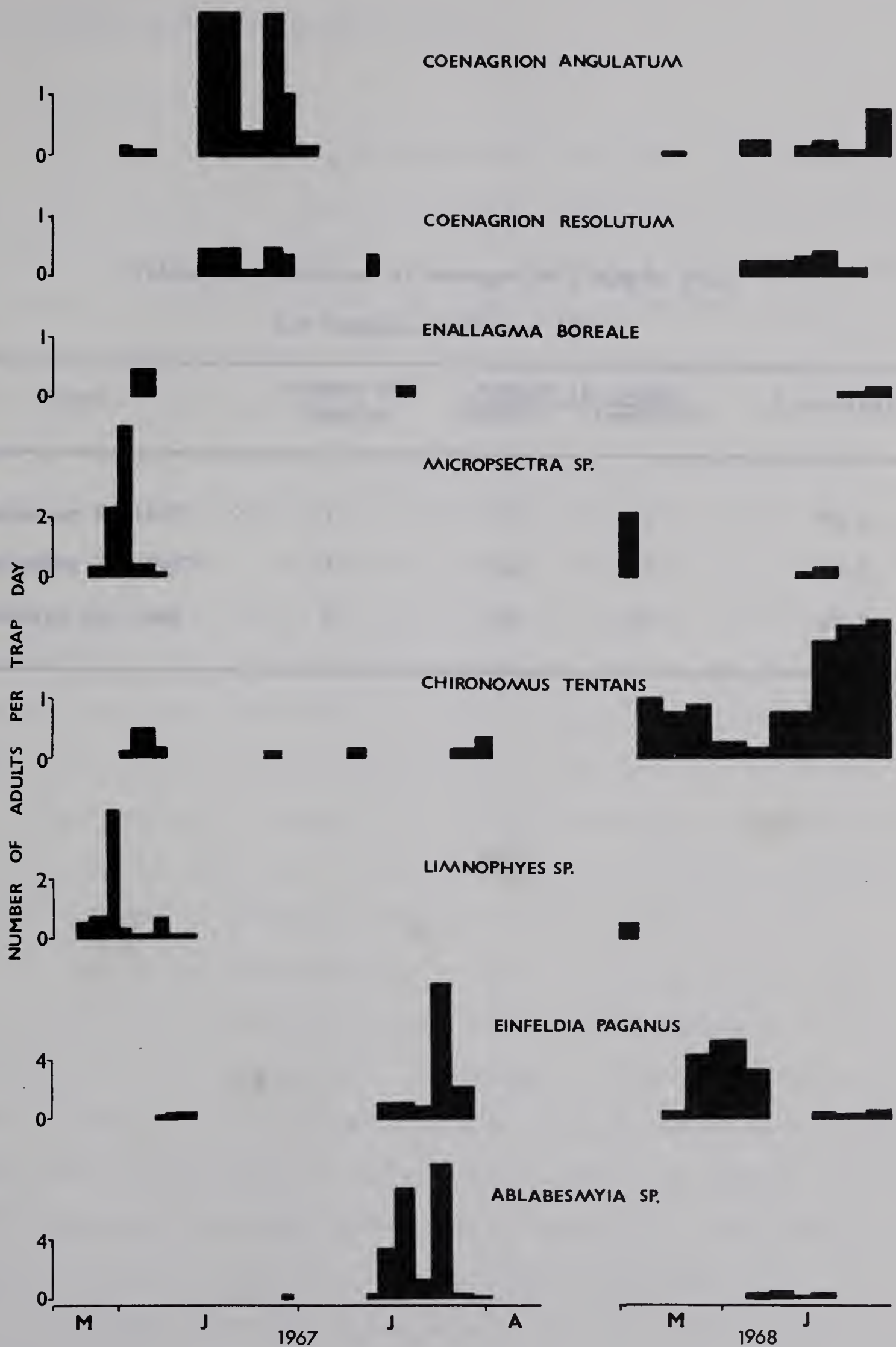


Table 10. *Survival of coenagrionid nymphs from
ice samples, 1967 and 1968*

Date	Number of Samples	Number of nymphs		% Survival
		Active	Immobile	
December 9, 1967	1	31	1	96.9
December 30, 1967	3	36	20	64.3
January 30, 1968	3	18	52	25.7

any method, despite an elaborate search.

e) Diptera

The family Chironomidae was numerically the largest single taxon in the fauna during 1967. Because even generic identification was impossible in the larval stages, the family must be treated as a single unit. Figure 23 shows the calculated numbers and biomass per square metre at each of the five sampling stations. It is immediately apparent that changes in abundance of chironomids can only be explained as a complex function of several factors, of which life-cycle changes and the drying out of the pond, with its concomitant redistribution of the larvae, were probably of great importance. One sampling point (IV) exhibited a comparatively stable biomass and density throughout the study, whereas others varied considerably. Some of the variation at III and V may be explained by migration of larvae from the south and east edges as the water receded each year, but the data are insufficient for more detailed examination.

When results for each month are combined, however, a more simplified picture appears (Table 11). It seems that the great increase in numbers for October 1967 is primarily a function of the introduction of young larvae from the previous reproductive season into the population, since the biomass does not increase in phase with numerical abundance. It is possible, however, that the above relationship is more apparent than real, for a clumped distribution might introduce more young larvae into a sample than would be representative of the pond as a whole. In addition, seasonal succession involving numerical dominance of species with small larvae would influence the ratio of biomass to numbers considerably.

In November, the single sample obtained was taken beneath an ice cover of 24 cm, and therefore the increase in both density and biomass was

Figure 23. *Number and biomass of Chironomidae at five sampling points, 1967 and 1968*

Open : Number per m²

Closed : Biomass (gm dry weight)/m²

I - V Sample points

1967

I

II

III

IV

V

JULY

10
0

3
0

AUG

10
0

3
0

SEPT

30
20
10
0

9
6
3
0

OCT

20
10
0
 $\text{NUMBER} / \text{M}^2 \times 10^{-3}$

6
3
0
GM DRY WEIGHT / M^2

NOV

20
10
0

6
3
0

1968

APR

10
0

3
0

MAY

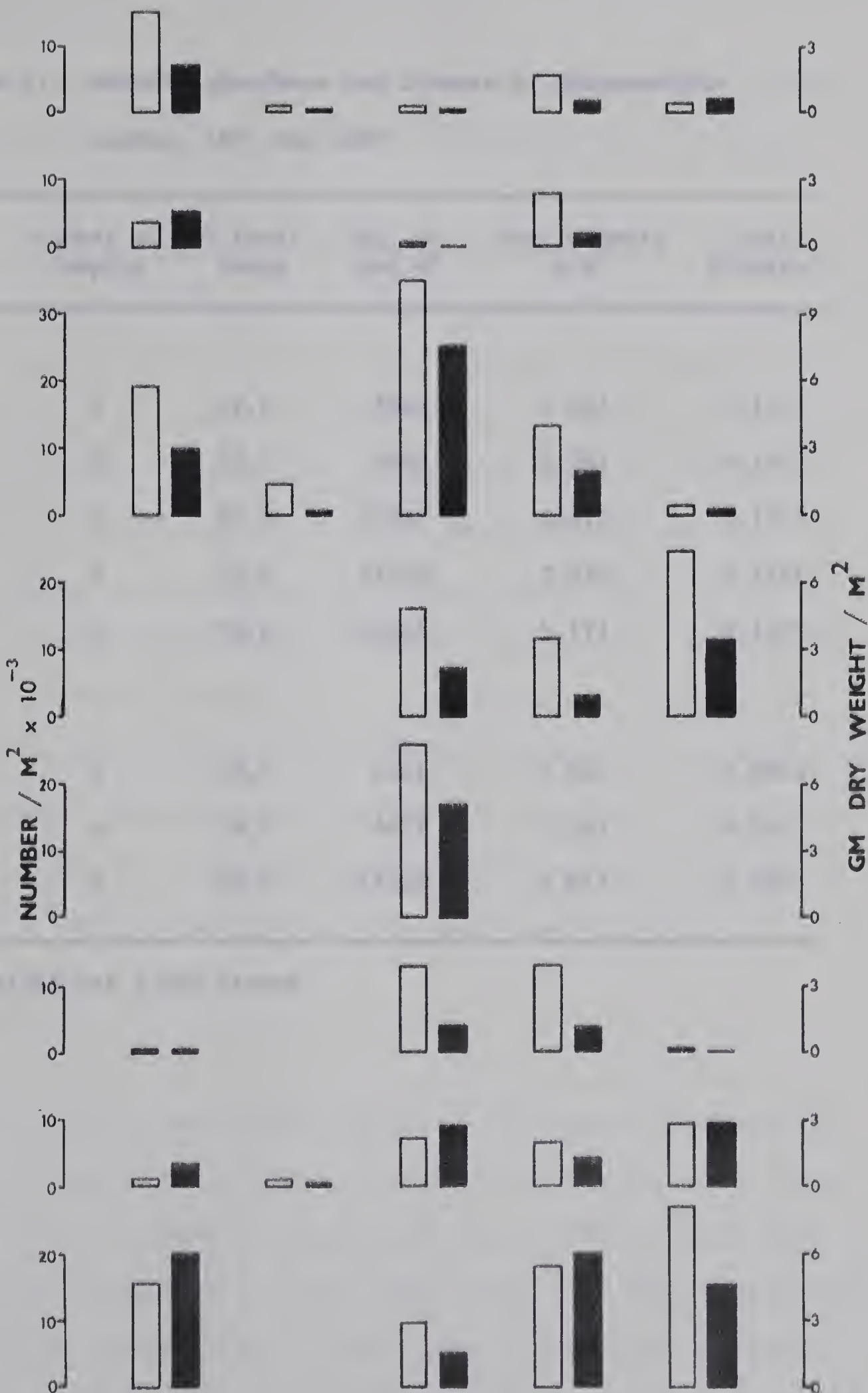
10
0

3
0

JUNE

20
10
0

6
3
0



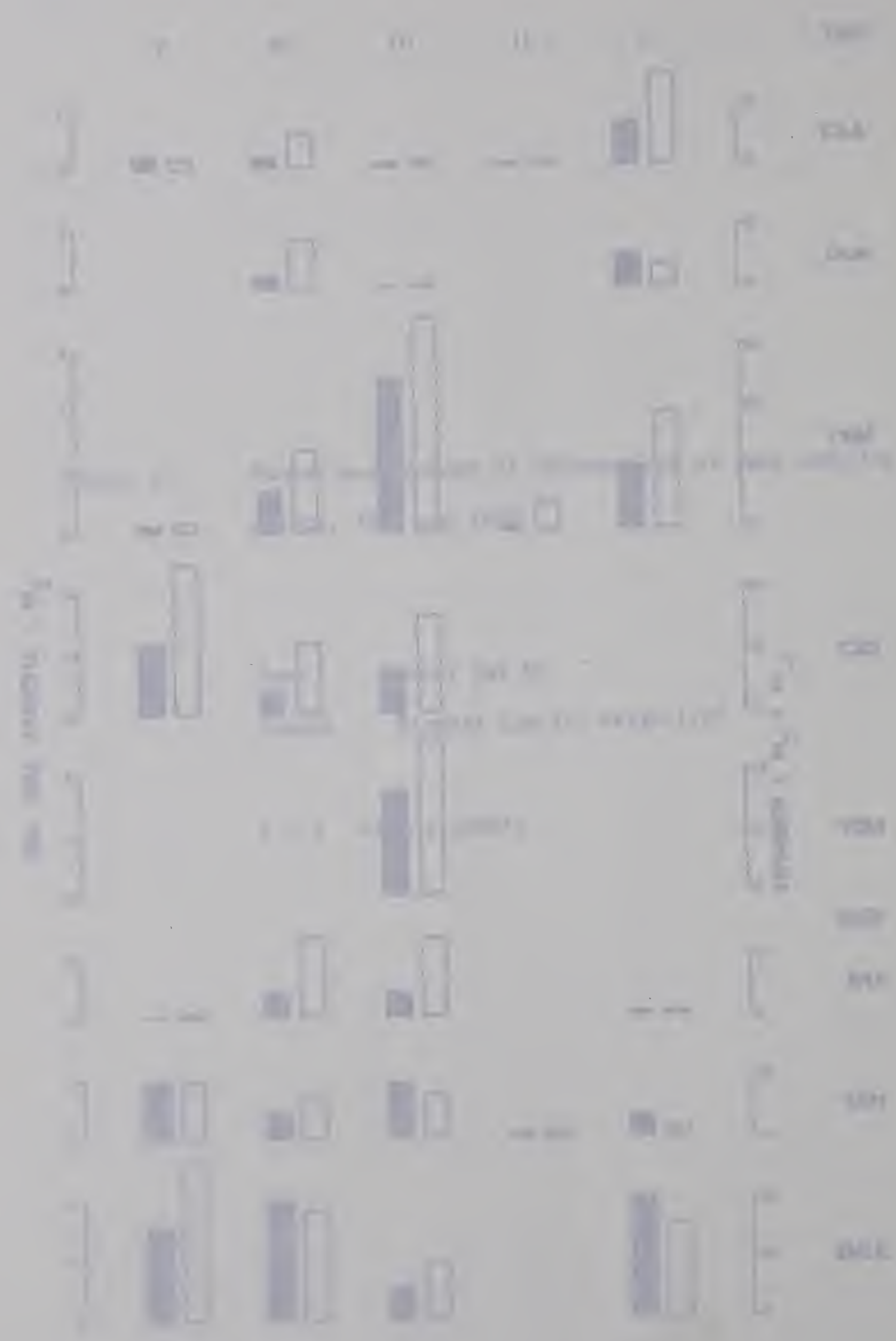


Table 11. *Monthly abundance and biomass of Chironomidae larvae, 1967 and 1968*

Month	Number of Samples	% Total Fauna	Avg. No. per m ²	Avg. biomass g/m ²	Unit biomass*
<u>1967</u>					
July	5	79.9	4860	0.814	0.1675
August	3	53.5	4050	0.781	0.1928
September	5	69.5	15047	2.613	0.1737
October	3	72.0	17788	2.278	0.1281
November	1	79.2	26244	5.171	0.1970
<u>1968</u>					
April	4	49.4	6561	0.632	0.0963
May	5	19.9	4977	1.602	0.3291
June	4	55.0	17423	4.517	0.2593

* g dry weight per 1,000 larvae

certainly the result, in part, of the migration of larvae to the deeper parts of the pond.

In 1968, the results seem to indicate rapid growth by the larvae between April and May, but this pattern disappeared with the active flight and reproductive period of June.

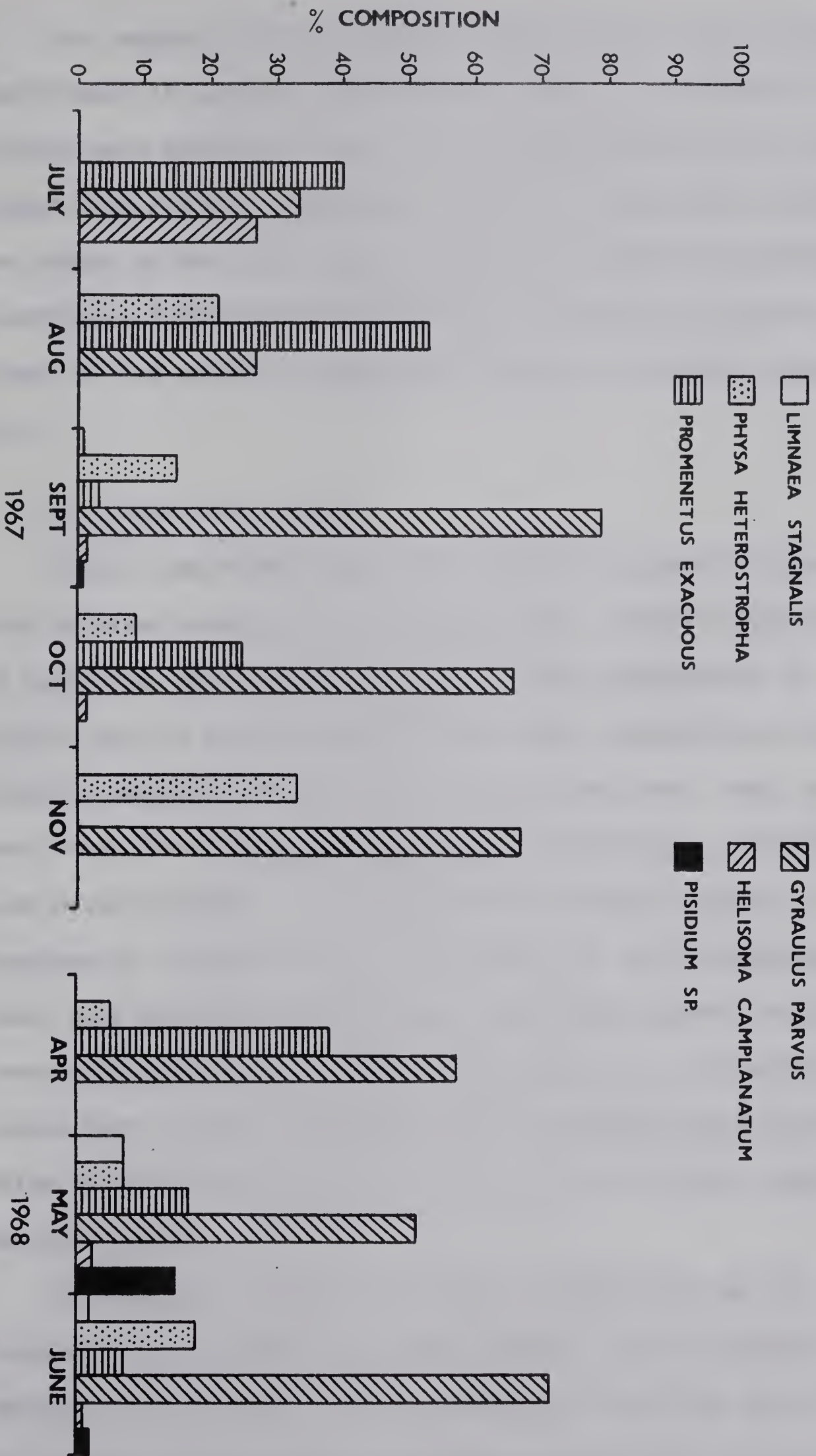
Emergence patterns for the five most abundant species support the contention that the community had changed drastically by 1968 (Fig. 22). Thus, *Chironomus tentans* Fabricius was considerably more numerous than in the previous year, whereas *Micropsectra* sp. was apparently less abundant in 1968 than before. On the basis of the early emergence period it is possible that *Einfeldia paganus* (Meigen) had also increased in numbers, but the situation with respect to the later flight period is unknown.

Several other Diptera occurred either consistently throughout the study, or in relative abundance for a short period. The larvae of *Palpomyia* sp. were included in most vertical samples, but the adults were never captured. *Chaoborus* sp. larvae were found in June of both years in very low numbers. Larvae and adults of *Aedes* sp. were collected in May and June, 1968, respectively, and a single adult *Anopheles* sp. in early June, 1968.

f) Mollusca

Molluscs were a conspicuous element of the fauna in both years, being represented by eight species of pulmonate gastropod and a single pelecypod. Total abundance varied from a low of 428/m² (July, 1967) to nearly 2,500/m² (September, October 1967; April, June 1968). Of the nine species, three — *Physa heterostropha*, *Promenetus exacuous* Say and *Gyraulus parvus* Say — were regularly more abundant than the others (Fig. 24), and usually constituted more than 65% of the total molluscan fauna.

Figure 24. *Relative numbers of six species of Mollusca,*
 1967 and 1968



Ice samples contained the same three species with occasional individuals of *Gyraulus crista* Linné; almost all individuals of these species were definitely alive. The average density of the four species together in all ice samples was 4,912/m², but the wide variation from one sample to the next clearly indicated a clumped distribution. Observation suggested that the number of molluscs was directly proportional to the amount of vegetation (mainly *L. trisulca*) trapped in the ice.

g) Other Invertebrates

Several important taxa of the community occurred in such low numbers that detailed examination is inappropriate. Of the Coleoptera, larvae of *Agabus* sp. and *Haliphus* sp. were commonly encountered in vertical samples and ice blocks throughout the study, and *Haliphus* adults were found in emergence traps in May 1967 and June 1968. Adult *Enochrus* sp. were taken from emergence traps in June of each year, although the larvae were never recorded. It is possible that several species, including *Enochrus* sp., *Laccophilus* sp., *Laccodytes* sp. and *Helophorus* sp., all of which were obtained only as adults, are regular summer immigrants, but never establish a sufficiently large population to be encountered in the larval form. A few *Callicorixa audeni* Hungerford and *Notonecta shooterii* Uhler adults were also obtained, but as with the above, immature stages were not found.

Trichoptera larvae of the family Limnephilidae and the genus *Triaenodes* were present in several samples, but total numbers were low. Emergence trap results, however, indicated that other families occurred in the pond : the phryganeid *Agrypnia pagetana* Curtis emerged in late May and early June 1967, to be followed by *Agraylea multipunctata* Curtis

(Hydroptilidae) in July. Adult *Triaenodes grisea* and *Triaenodes* sp. were only found in late June, 1968.

A great variety of Acari were seen or collected at the pond in both years. Three genera have been provisionally identified: *Eylais*, *Forelia* and *Hydrachna* — but an extensive examination would undoubtedly reveal the presence of several more. Immature stages were frequently observed on the venter of the thorax of most emerging Zygoptera, but these were not identified.

5. Vertebrates

The vertebrate fauna of the pond was restricted entirely to seasonal visitors. In the first year a pair of horned grebes (*Podiceps aurita*) and two pairs of coots (*Fulica americana*) established nests on or near the pond; in 1968 a pair of grebes returned at the end of May but, presumably as a result of the low water level, were absent by the end of June. Many other waterfowl, including mallards, *Anas platyrhynchos platyrhynchos* L., pintails, *A. acuta* L., blue-winged teal, *A. discors discors* L., and lesser scaup, *Aythya affinis* (Eyton), visited the pond daily, flying in from nearby lakes at dawn and leaving at dusk.

Muskrats, *Ondatra zibethicus* (Osgood), invaded the pond toward the end of the summer and caused considerable trouble by destroying emergence traps. As a result of the total freezing of the pond in winter, however, none overwintered there.

In the spring of both years large numbers of the chorus frog, *Pseudacris nigrita*, spawned in the pond, but in the second year the rapid withdrawal of water left many egg masses dry before the young had hatched. Despite the very large numbers of eggs laid, no tadpole was ever obtained in vertical samples, and it is considered that survival was low. In 1968 a pair of tiger salamanders, *Ambystoma tigrinum*, were seen.

DISCUSSION

The changes in physical characteristics of the pond indicate that it is highly susceptible to variations in climatic conditions. During the study period, weather conditions deviated considerably from the long-term averages. Thus, in 13 months, a decrease of 33% in precipitation (Fig. 5) and increases of 6.5 and 11.9% in total wind mileage and duration of bright sunshine respectively (Appendix VII), resulted in the loss of more than 90% of the springtime volume of the pond. Ponds of this size undergo considerable reduction in volume during the course of each summer, but consideration of biological phenomena recorded here suggests that the recession of the water level was more severe in 1967 and 1968 than in most years. As a result, the morphometric characteristics of the pond in June, 1968, more closely resembled those of astatic or vernal ponds of the area than permanent water bodies.

The total freezing of the water in the basin during winter, which has certainly occurred for the three years 1966 through 1968, is a distinctive phenomenon which is probably to be found in many permanent, shallow ponds in western Canada. Unfortunately, however, it is a phenomenon which has been largely unrecorded and totally unstudied. Dineen (1953) reported a single instance in Minnesota in the winter of 1949-50, with the observation that a species of *Physa* apparently died out as a result. Total freezing of pond water is certainly more common in higher latitudes, but other than the physiological study on *Chironomus* sp. larvae found in the ice of a pond at Point Barrow, Alaska (Scholander *et al.*, 1953), nothing is known of the importance of freezing to the aquatic fauna inhabiting such ponds.

Detailed examination of the process of freezing conducted in this

study demonstrated, with regard to the fate of inorganic ions, that there was no essential difference between the freezing of natural fresh and sea water. Thus, as water changes state the ions and dissolved or suspended particulate matter are largely excluded from the ice and therefore become more concentrated in the underlying water. This is certainly the explanation of the increase in ionic concentration recorded in shallow, eutrophic lakes in central Alberta (for example, by Kerekes, 1965). It is not known, as yet, if this phenomenon is of any great significance to the fauna inhabiting such shallow lakes, but with respect to oxygen concentration this seems highly probable. It has been shown that the water beneath the ice may become supersaturated (Table 7) as ice thickness increases. Thus, the abundance of oxygen immediately beneath the ice cover relative to the level in water at lower levels is probably the explanation for the high concentration of invertebrates frequently found just below the ice in lakes and streams during winter.

One aspect of these results deserves further consideration. Paterson (1966) and Bozniac and Kennedy (1968) have postulated that selective uptake of orthophosphate by ice may occur, resulting in higher concentrations in ice than in water. No evidence for such a phenomenon has been obtained in the present study, although the pattern of distribution of orthophosphate was more variable than that exemplified by other ions. In March 1968, however, the orthophosphate concentration of the water was very high compared with its abundance in 1967 (Fig. 7), and then decreased rapidly in April. The origin of this orthophosphate is unknown, but it seems likely that it is a product of the decomposition of organic material formed during the previous year. In any event, the ecological significance of this high concentration in spring, with respect to its importance in the development of plankton blooms, is hardly to be doubted (Bozniac and

Kennedy, 1968; Lin, 1968).

It is clear from the present results that the phytoplankton was usually dominated by a single species (Fig. 15). In June 1967, *Aphanizomenon flos-aquae* occurred in bloom proportions, but the bloom ended by the middle of July, and thereafter the total abundance of all phytoplankton species was less than 5% of this June maximum. Thus, while autotrophic organisms were present throughout the year, measurable changes in the concentration of dissolved oxygen which could be attributed to primary production were only recorded in early July, and for the remaining months oxygen saturation was considered to be a complex function of limited photosynthesis, decomposition and wind activity. It is not known if this restricted pattern of primary production is typical of the pond, but in view of similar results obtained by Dineen (1953) for a pond in Minnesota, it seems highly possible. If this is true, therefore, the limited period of high primary production in early spring represents a very different ecological situation from the succession of phytoplankton pulses recorded by Hammer (1964) and Lin (1968) for shallow lakes in western Canada. In these lakes, seasonal succession of algae results in a high level of photosynthesis that is maintained through most of the summer, the ratio between maximum and minimum phytoplankton concentrations being of the order of four or five to one (Rawson, 1953). Such multi-species associations and successions exhibit a high degree of 'order' in the sense used by Petruszewicz (1966) and Margalef (mimeographed paper), and seasonal succession of organisms may therefore be taken as an index of the stability of the community in the same sense that the more complex energy relationships of the tropics are more stable than systems in higher latitudes (Dunbar, 1960 and 1968). By comparison, the extreme limitation

of primary production in the pond examined here, is to be regarded as indicative of an unstable community.

The absence of a bloom in 1968, and the apparent replacement of *Aphanizomenon flos-aquae* by *Spirogyra* sp. and *Anabaena spiroides* in that year (Fig. 15) were important changes which completely altered the productivity of the ecosystem. They were accompanied by distinct changes in the invertebrate community. Thus, *Keratella cochlearis*, abundant in 1967, was relatively uncommon in the second year (Fig. 16), *Diaptomus leptopus* was replaced by *D. franciscanus* (Fig. 17), and *Lumbriculus variegatus* by *Chaetogaster diaphanus* (Fig. 18). Among the insects, *Caenis simulans* and *Cloeon* sp. were not collected in 1968, *Coenagrion angulatum*, *C. resolutum* and *Enallagma boreale* gave way to species of *Lestes* (Fig. 21), and distinct differences were apparent in the abundance of emerging Diptera (Fig. 22).

It is not known how often in the past species replacement of this magnitude has occurred, but the rapid success of invaders indicates that the pond community was always subject to immigration by the same or similar species. Thus, the extensive replacement of one species by another, as recorded here, may be either a characteristic phenomenon of ponds of this kind, or an indication of transient ecological succession under exceptional weather conditions. Lack of research on the ecology of natural shallow ponds, however, makes it impossible to determine which situation is most likely in this instance.

If the first alternative is valid, the pond community must be interpreted as an extremely unstable one. Accordingly, the specific faunal and floral associations occurring in each summer would be determined as a fortuitous assemblage selected from the successful immigrants or residents

of the previous year by the environmental conditions prevailing during the following spring. In this case, the distinction between a permanent or characteristic fauna and an adventitious one is meaningless.

The distinct association of some of the 1968 community with astatic waters (particularly *Chaetogaster diaphanus* and the genus *Lestes*), however, seems to imply that the pond community has undergone a definite, if temporary, transition from an association of species typical of permanent ponds to one more characteristic of vernal waters. This is clearly related to the recorded changes in morphometric characteristics, and suggests an increase in the vulnerability (cf. Elton, 1966) of the community to invasion.

Ecological succession is generally accepted as a real, if poorly understood, phenomenon (Clements, 1916; Gleason, 1927; Whittaker, 1953; Dunbar, 1968), and it may even be a necessary feature of ecosystems (Bellamy and Rieley, 1967; Bellamy and Clarke, 1968). Thus, given sufficient time, a lake is expected to pass through a series of stages, from oligotrophy through eutrophy, until the basin is completely filled and terrestrial succession begins (Lindemann, 1942). The very distinctiveness of these stages testifies to a varying degree of stability throughout this sequence: community stability becomes less as the ecosystem approaches a transition zone between successive stages, so that rather small changes in environmental conditions greatly influence the rate of development from one stage to the next.

The major faunal changes recorded in this study are thus indicative of an unstable and highly vulnerable community, which, under the influence of changing climate or human activities for example, may exhibit rapid progressive or retrogressive succession. During the present study, the change was clearly progressive, in that the ecosystem adopted characteristics

associated with temporary pools, but there is no guarantee that subsequent years of normal precipitation and heat budget would not reverse the procedure.

LITERATURE CITED

- A.P.H.A. 1960. Standard methods for the examination of water and wastewater. 11th ed. American Public Health Association, New York. 626 p.
- Anonymous. 1967. Monthly meteorological summary. Meteorological Branch, Dept. of Transport, Edmonton.
- Arnol'd-Aliab'ev, V.I. 1933. The chemical nature of ice in the Gulf of Finland as based on its strength. *Izvestija Instituta Obshchey i Neorganicheskoy Khimii*. 6:229-233. (Abstr. in S.I.P.R.E. Bibliography.)
- Bartow, E. 1913. The sanitary-chemical and bacteriological examination of natural ice. *Proc. Nat. Ice Assoc. America*. 87-93. (Abstr. in S.I.P.R.E. Bibliography.)
- Bayrock, L.A. and G.M. Hughes. 1962. Surficial geology of the Edmonton district, Alberta. Preliminary Report 62-6, Research Council of Alberta, Edmonton, Alberta. 40 p. 4 maps.
- Bellamy, D.J. and J. Rieley. 1967. Some ecological statistics of a "miniature bog". *Oikos* 18:33-40.
- Bellamy, D.J. and P.H. Clarke. 1968. Application of the second law of thermodynamics and Le Chatelier's Principle to the developing ecosystem. *Nature* 218:1180.
- Bennington, K.O. 1967. Desalination features in natural sea ice. *J. Glaciology* 6:845-857.
- Bird, R.D. 1961. Ecology of the aspen parkland of western Canada in relation to land use. Contribution #27, Research Station, Canada Dept. of Agriculture, Winnipeg, Man. 155 p.
- Bowser, W.E., A.A. Kjearsgaard, T.W. Peters and R.E. Wells. 1962. Soil survey of Edmonton, Sheet 83-H. Alberta Soil Survey Report #21. University of Alberta Bulletin #55-4 Edmonton. 66 p. 3 maps.
- Bozniac, E.G. and L.L. Kennedy. 1968. Periodicity and ecology of the phytoplankton in an oligotrophic and eutrophic lake. *Canad. J. Bot.* 46:1259-1271.
- Brinkhurst, R.O. 1967. Sampling the benthos. Mimeo. P.R.32 Great Lakes Institute, University of Toronto. 6 p.
- Brown, S.R. 1956. A piston sampler for surface sediments of lake deposits. *Ecology* 37:611-613.
- Budd, A.C. and K.F. Best. 1964. Wild plants of the Canadian prairies. Publication 983, Research Branch, Canada Dept. of Agriculture, Ottawa. 519 p.

- Buscemi, P.A. 1958. Littoral oxygen depletion produced by a cover of *Elodea canadensis*. *Oikos* 9:239-245.
- Chernigovskii, N. 1939. The alkalinity of sea ice in the B. Vilkitski Strait. *Problemy Arktiki* 7-8:123-125. Abstr. in S.I.P.R.E. Bibliography.
- Clements, F.E. 1916. Plant succession. Pub.#242, Carnegie Institute of Washington. 521 p.
- Cole, G.A. 1967. Contrasts among calanoid copepods from permanent and temporary ponds in Arizona. *Am. Midl. Nat.* 76:351-368.
- Cummins, K.W. 1962. An evaluation of some techniques for the collection and analysis of benthic samples with special emphasis on lotic waters. *Am. Midl. Nat.* 67:477-502.
- Dineen, C.F. 1953. An ecological study of a Minnesota pond. *Am. Midl. Nat.* 50:349-376.
- Dorsey, N.E. 1940. Properties of ordinary water substance in all its phases. Amer. Chem. Soc. Monogr. Ser. Reinhold, New York. 673 p.
- Dunbar, M.J. 1960. The evolution of stability in marine environments. Natural selection at the level of the ecosystem. *Am. Nat.* 94:129-136.
- Dunbar, M.J. 1968. Ecological development in polar regions. Prentice-Hall, New York. 100 p.
- Dzens-Litovskii, A.L. 1954. Salt transport by wind. *Trudy Laboratorii Ozerovedeniya Akademii Nauk S.S.S.R.* 3:127-149. Abstr. in S.I.P.R.E. Bibliography.
- Elgmork, K. 1962. A bottom sampler for soft mud. *Hydrobiologia* 20:167-172.
- Elton, C.S. 1966. The pattern of animal communities. Methuen, London. 432 p.
- Gerking, S.D. 1957. A method of sampling the littoral macrofauna and its application. *Ecology* 38:219-226.
- Gleason, H.A. 1927. Further views on the succession concept. *Ecology* 8:299-326.
- Greenbank, J.T. 1945. Limnological conditions in ice-covered lakes, especially as related to winter-kill of fish. *Ecol. Monogr.* 15:345-390.
- Hammer, U.T. 1964. The succession of "bloom" species of blue-green algae and some causal factors. *Verh. Internat. Verein. Limnol.* 15:829-836.
- Hartland-Rowe, R. 1966. The fauna and ecology of temporary pools in western Canada. *Verh. Internat. Verein. Limnol.* 16:577-584.

- Horne, F. 1967. Effects of physical-chemical factors on the distribution and occurrence of some southeastern Wyoming phyllopoeds. *Ecology* 48:472-477.
- Hutchinson, G.E. 1957. A treatise on limnology. Vol. I. Wiley, New York. 1015 p.
- Hutchinson, G.E. 1965. The ecological theater and the evolutionary play. Yale Univ. Press, New Haven. 139 p.
- Hutchinson, G.E. 1967. A treatise on limnology. Vol. II. Wiley, New York. 1115 p.
- Jenkin, B.M. and C.H. Mortimer. 1938. Sampling lake deposits. *Nature*, London. 142:834-835.
- Jewell, M.E. 1927. Aquatic biology of the prairie. *Ecology* 8:289-298.
- Kenk, R. 1949. The animal life of temporary and permanent ponds in southern Michigan. *Misc. Publs. Mus. Zool. Univ. Mich.* 71:1-66.
- Kerekes, J. 1965. A comparative limnological study of five lakes in central Alberta. M.Sc. Thesis, Dept. of Zoology, Univ. of Alberta, Edmonton. 164 p.
- Kutkuhn, J.H. 1958. Notes on the precision of numerical and volumetric plankton estimates from small-sample concentrates. *Limnol. and Oceanogr.* 3:69-83.
- Laycock, A.H. 1968. The water balance of the Gull Lake Basin -- a system analysis for the period 1921-1968. Mimeo. 38 p.
- Lei, C. L. 1968. Field and laboratory studies of *Daphnia schødleri* Sars from Big Island Lake, Alberta. M.Sc. Thesis, Dept. of Zoology, Univ. of Alberta, Edmonton. 149 p.
- Lin, C. K. 1968. Phytoplankton succession in Astotin Lake, Elk Island National Park, Alberta. M.Sc. Thesis, Dept. of Botany, Univ. of Alberta, Edmonton. 148 p.
- Lindeman, R.L. 1942. The trophic-dynamic aspect of ecology. *Ecology*. 23:399-418.
- Lippert, B.E. and D.L. Jameson. 1964. Plant succession in temporary ponds of the Willamette Valley, Oregon. *Am. Midl. Nat.* 71:181-197.
- Livingstone, D.A. 1955. A lightweight piston sampler for lake deposits. *Ecology* 36:137-139.
- Lliboutry, L. 1964. Texture crystalline et deformation plastique de la glace. *J. Hydraulic Research* 2:41-49.
- Macan, T.T. 1963. Freshwater ecology. Wiley, New York. 338 p.

- Malmgren, F. 1927. On the properties of sea-ice. John Griegs Boktrykkeri, Bergen. 67 p. Abstr. in S.I.P.R.E. Bibliography.
- Margalef, R. (n.d.) Successions of populations. Mimeo. 32 p.
- Menon, P.S. 1966. Population ecology of *Gammarus lacustris* Sars in Big Island Lake. Ph.D. Thesis, Dept. of Zoology, Univ. of Alberta, Edmonton. 117 p.
- Moore, J.E. 1964. Notes on the leeches (*Hirudinea*) of Alberta. Nat. Mus. Canada. Nat. Hist. Paper #27 1-15.
- Moore, J.E. 1966. Further notes on Alberta leeches (*Hirudinea*). Nat. Mus. Canada. Nat. Hist. Paper #32 1-11.
- Morgan, N.C. and A. B. Waddell. 1961. Insect emergence from a small trout loch and its bearing on the food supply of fish. Scient. Invest. Fishery Bd. Scotl. 25:1-39.
- Morgan, N.C., A.B. Waddell and W. B. Hall. 1963. Comparison of the catches of emerging aquatic insects in floating box and submerged funnel traps. J. Anim. Ecol. 32:203-219.
- Mozley, A. 1932. A biological study of a temporary pond in western Canada. Am. Nat. 66:236-249.
- Nelson, K.H. and T. G. Thompson. 1953. Desalting of water by freezing processes. Tech. Rep. #13, Dept. of Oceanography, Univ. of Washington. 22 p.
- Nelson, K.H. and T. G. Thompson. 1954. Deposition of salts from seawater by frigid concentration. Tech. Rep. #29, Proj. NR083012, Dept. of Oceanography, Univ. of Washington. 30 p.
- Paterson, C.G. 1966. The limnology of the North Saskatchewan River near Edmonton. M.Sc. Thesis, Dept. of Zoology, Univ. of Alberta, Edmonton. 126 p.
- Petrusewicz, K. 1966. Dynamics, organisation and ecological structure of population. Ekologia Polska 14:413-436.
- Pinsent, M.E. 1967. A comparative limnological study of Lac La Biche and Beaver Lake, Alberta. M.Sc. Thesis, Dept. of Zoology, Univ. of Alberta, Edmonton. 147 p.
- Pounder, E.R. 1965. The physics of ice. Pergamon, Oxford. 151 p.
- Rawson, D.S. 1942. A comparison of some large alpine lakes in western Canada. Ecology 23:143-161.
- Rawson, D.S. 1953. The standing crop of net plankton in lakes. J. Fish. Res. Bd. Can. 10:224-237.
- Reid, G.K. 1961. Ecology of inland waters and estuaries. Reinhold, New York. 375 p.

- Rodhe, W. 1949. The ionic composition of lake waters. *Verh. Internat. Verein. Limnol.* 10:377-386.
- Ruediger, G.F. 1913. A study of the purity of natural ice from polluted water. *Proc. Nat. Ice Assoc. America.* 68-73. Abstr. *in* S.I.P.R.E. Bibliography.
- Scholander, P.F., W. Flagg, R.J. Hock and L. Irving. 1953. Studies on the physiology of frozen plants and animals in the Arctic. *J. Cell Comp. Physiol.* 42 (Suppl.1):1-56.
- Schulz, B. 1930. Investigations of the properties of sea ice by the "Maud" Expedition. *Ann. Hydrographie u. Maritim. Meteorologie.* 58:20-24. Abstr. *in* S.I.P.R.E. Bibliography.
- Scott, J.T. and R.A. Ragotzkie. 1961. The heat budget of an ice-covered inland lake. Tech. Rep. 6 ONR Contract No. 1202 (07). Univ. of Wisconsin, Dept. of Meteorology, Madison, Wisc.
- Scott, J.T. 1964. A comparison of the heat balance of lakes in winter. Tech. Rep. 13 ONR Contract No. 1202 (07). Univ. of Wisconsin, Dept. of Meteorology, Madison, Wisc.
- S.I.P.R.E. Bibliography. Snow, Ice and Permafrost Establishment. Willmette, Illinois. (Now U.S. Army Cold Regions Laboratory, Corps of Engineers, Hanover, N.H.)
- Southwood, T.R.E. 1966. *Ecological methods.* Methuen, London. 391 p.
- Sparks, J.C. 1910. Water from melted ice for domestic use. *Proc. Nat. Ice Assoc. America.* 34-38. Abstr. *in* S.I.P.R.E. Bibliography.
- Sverdrup, H.V. 1926. Scientific work of the "Maud" Expedition 1922-25. *Naturen* 50:161-180. Abstr. *in* S.I.P.R.E. Bibliography.
- Tyndall, J. 1898. *The forms of water in clouds and rivers, ice and glaciers.* Appleton, New York. 196 p.
- Vallentyne, J.R. 1955. A modification of the Livingstone piston sampler for lake deposits. *Ecology* 36:139-141.
- Walker, E.M. 1953. *The Odonata of Canada and Alaska Vol. I.* Univ. of Toronto. 292 p.
- Welch, P.S. 1948. *Limnological methods.* McGraw-Hill, New York. 381 p.
- Whittaker, R.H. 1953. A consideration of climax theory. *Ecol. Monogr.* 23:41-78.
- Wiese, W. 1930. The salts contained in sea ice. *Ann. Hydrographie u. Maritim. Meteorologie.* 58:282-286. Abstr. *in* S.I.P.R.E. Bibliography.
- Zubov, N.N. 1945. Changes in the temperature and the salinity of the ocean. *L'dy Arktiki. Izd-vo Glavsevmorputi, Moscow.* 19-48. Abstr. *in* S.I.P.R.E. Bibliography.

APPENDIX I

*Provisional list of organisms identified from the study area
with months in which they were seen or collected*

Key:	+ present - not recorded		A adult(s) N nymph(s)							L larva(e)					
			1967							1968					
	M	J	J	A	S	O	N	D		J	F	M	A	M	J
Myxophyceae															
<i>Aphanizomenon flos-aquae</i>	+	+			+	-	-	-		-		-	-	-	-
<i>Anabaena spiroides</i>	-	+			-	+	-	-		-		-	-	-	+
Chlorophyceae															
<i>Eudorina</i> sp.	+	+			+	-	-	-		-		-	+	-	-
<i>Volvox</i> sp.	+	+			+	-	-	-		-		-	+	-	-
<i>Chlorococcum</i> sp.	-	-			-	-	-	-		-		+	-	-	-
<i>Golenkinia paucispina</i>	-	-			-	+	-	-		-		-	-	-	-
<i>Pediastrum</i> sp.	-	-			+	-	+	-		+		-	-	-	+
<i>Tetraedron</i> sp.	-	-			-	-	+	-		-		-	-	-	-
<i>Ankistrodesmus</i> sp.	-	-			-	+	+	-		-		-	-	+	-
<i>Treubaria</i> sp.	-	-			-	-	-	-		-		+	-	-	-
<i>Scenedesmus</i> sp.	-	-			-	-	+	-		+		-	-	+	-
<i>Actinastrum</i> sp.	-	-			-	-	-	-		+		-	-	-	-
<i>Staurastrum</i> sp.	-	-			+	+	+	+		+		-	+	-	-
<i>Euastrum</i> sp.	-	-			+	-	-	-		+		-	-	-	-
<i>Closterium</i> sp.	-	-			-	-	-	-		-		-	-	+	-
<i>Cosmarium</i> sp.	+	-			+	-	+	+		+		-	+	+	+
<i>Spirogyra</i> sp.	-	+			+	-	-	-		-		-	+	+	+
Dinophyceae															
<i>Peridinium</i> sp.	-	-			-	+	-	-		-		-	-	-	-
<i>Gonyaulax</i> sp.	-	-			-	-	-	-		+		+	+	-	-

	M	J	J	A	S	O	N	D	J	F	M	A	M	J
Bacillariophyceae														
<i>Tabellaria</i> sp.	-	-			+	-	-	-	+		+	-	+	+
<i>Meridion</i> sp.	-	-			-	-	+	-	+		-	+	+	+
<i>Fragilaria</i> sp.	+	+			+	+	+	+	+		+	+	+	+
<i>Cocconeis</i> sp.	-	-			-	-	-	-	+		+	+	+	+
<i>Cylindrotheca</i> sp.	-	-			-	-	-	-	+		-	+	+	+
<i>Epithemia</i> sp.	-	-			+	-	+	-	+		-	+	+	+
<i>Diatomella</i> sp.	-	-			-	-	+	-	-		-	-	-	-
<i>Diploneis</i> sp.	-	-			-	-	+	-	+		-	+	+	+
<i>Amphipleura</i> sp.	-	-			-	+	-	-	+		+	+	+	+
<i>Pinnularia</i> sp.	-	-			-	+	+	-	+		+	+	+	+
<i>Brebissonia</i> sp.	-	-			+	+	+	+	+		-	+	+	-
<i>Stauroneis</i> sp.	-	-			-	-	+	-	-		-	-	-	-
<i>Navicula</i> sp. (<i>N. petersenii</i> ?)	-	-			-	-	+	-	+		-	-	-	-
<i>Navicula</i> sp. (<i>N. digitoradiata</i> ?)	-				-	-	+	-	+		-	-	+	-
<i>Gomphonema</i> sp.	-	-			-	-	+	-	+		-	+	+	-
<i>Cymbella</i> sp.	-	-			-	-	+	-	+		-	+	-	-
Coelenterata - Hydrozoa														
<i>Hydra</i> sp.	-	-	-	-	+	+	-	-	-		-	-	-	-
Aschelminthes - Rotifera														
<i>Filinia longiseta</i>	+	-			+	+	-	-	-		-	+	-	-
<i>Ascomorpha</i> sp. (<i>A. ecaudis</i> ?)	-	-			-	-	-	-	-		-	+	-	-
<i>Keratella cochlearis</i>	+	+			+	+	-	-	-		-	+	-	+
<i>Keratella quadrata</i>	+	+			-	-	-	-	-		-	+	+	+
<i>Notholca</i> sp.	-	-			+	-	-	-	-		-	+	-	+
<i>Trichocerca</i> sp. (<i>T. cylindrica</i> ?)	-				+	+	-	-	-		-	-	-	-
<i>Colurella obtusa</i> ?	-	-			+	-	-	-	-		-	-	-	-

	1967								1968					
	M	J	J	A	S	O	N	D	J	F	M	A	M	J
Aschelminthes - Rotifera (cont'd)														
<i>Trichotria</i> sp.	-	+			+	-	-	-	-		-	-	-	-
<i>Brachionus bidentata</i>	-	-			+	-	-	-	-		-	-	-	-
<i>Mytilina</i> sp.	-	-			-	-	-	-	-		-	-	+	+
<i>Monostyla lunaris</i>	-	+			+	+	-	-	-		-	+	+	+
 Annelida - Oligochaeta														
<i>Lumbriculus variegatus</i>	+	-	+	+	+	+	+	-	-		-	+	+	+
<i>Chaetogaster diaphanus</i>	-	-	-	-	-	-	-	-	-		-	+	+	+
 Annelida - Hirudinea														
<i>Oculobdella lucida</i>	+	-	-	+	-	-	-	-	-		-	+	-	-
<i>Glossiphonia complanata</i>	+	+	-	-	-	-	-	-	-		-	-	-	-
<i>Glossiphonia heteroclita</i>	+	-	-	-	+	+	-	-	-		-	-	+	+
<i>Helobdella fusca</i>	+	-	-	-	-	-	-	+	-		-	+	+	+
 Arthropoda - Crustacea - Anostraca														
<i>Eubranchipus bundyi</i>	-	-	-	-	-	-	-	-	-		-	+	-	-
 Arthropoda - Crustacea - Conchostraca														
<i>Lynceus mucronatus</i>	+	+	-	-	-	-	-	-	-		-	-	+	+
 Arthropoda - Crustacea - Cladocera														
<i>Polyphemus pediculus</i>	-	-	-	-	-	-	-	-	-		-	-	+	-
<i>Daphnia rosea</i>	-	-	+	+	+	+	-	-	-		-	+	+	+
<i>Daphnia pulex</i>	-	+	+	+	+	+	-	-	-		-	-	+	+
<i>Daphnia catawba</i>	-	-	+	+	-	+	-	-	-		-	-	+	+
<i>Scapholeberis kingi</i>	-	-	-	-	-	-	-	-	-		-	-	+	-
<i>Moinodaphnia</i> sp.	-	-	-	-	-	-	-	-	-		-	-	+	+

Arthropoda - Crustacea - Cladocera (cont'd)	1967								1968					
	M	J	J	A	S	O	N	D	J	F	M	A	M	J
<i>Bosmina longirostris</i>	-	+	-	+	+	+	-	-	-		-	-	+	+
<i>Graptoleberis testudinaria</i>	-	-	-	-	-	-	-	-	-		-	-	+	+
<i>Simocephalus vetulus</i>	-	-	-	-	-	-	+	+	-		-	+	-	+
Arthropoda - Crustacea - Ostracoda														
<i>Cyclocypris ampla</i>	-	-	-	-	+	-	-	+	+		-	+	-	-
<i>Candona</i> sp.	-	-	-	-	+	+	+	+	+		-	+	+	-
<i>Cypris</i> sp.	-	-	-	-	-	-	-	-	-		-	-	+	+
Arthropoda - Crustacea - Copepoda														
<i>Diaptomus leptopus</i>	+	+	+	+	+	-	-	-	-		-	-	-	-
<i>Diaptomus franciscanus</i>	-	-	-	-	-	-	-	-	-		-	+	+	-
<i>Mesocyclops</i> sp.	-	-	-	-	+	+	-	+	+		-	+	+	+
Arthropoda - Crustacea - Amphipoda														
<i>Hyalella azteca</i>	-	-	-	-	+	-	-	-	-		-	-	-	+
<i>Gammarus lacustris</i>	+	-	-	-	+	-	-	-	-		-	-	-	-
Arthropoda - Insecta - Ephemeroptera														
<i>Caenis simulans</i>	N	-	A	-	N	N	N	N	N		-	-	-	-
<i>Cloeon</i> sp.	-	-	N	N	N	N	N	N	-		-	-	-	-
Arthropoda - Insecta - Odonata														
<i>Anax</i> sp.	-	-	-	N	-	-	-	-	-		-	-	-	-
<i>Aeshna</i> sp.	-	-	A	-	-	-	-	-	-		-	-	-	-
<i>Brachymesia</i> sp.	-	-	A	A	-	-	-	-	-		-	-	-	-

	1967								1968					
	M	J	J	A	S	O	N	D	J	F	M	A	M	J
Arthropoda - Insecta - Diptera - Heleinae														
<i>Palpomyia</i> sp.	L	-	L	L	L	L	L	L	L		L	L	-	L
<i>Stilobezzia</i> sp.	-	-	-	-	-	-	-	-	-		-	L	-	A
Arthropoda - Insecta - Diptera - Chironomidae														
<i>Chironomus hyperboreus</i>	A	A	-	-	-	-	-	-	-		-	A	A	-
<i>Chironomus tentans</i>	-	A	A	A	-	-	-	-	-		-	-	A	A
<i>Psectrocladius</i> sp. 1	-	A	-	-	-	-	-	-	-		-	-	-	A
<i>Psectrocladius</i> sp. 2	-	-	-	-	-	-	-	-	-		-	-	A	-
<i>Tanytarsus</i> sp.	-	-	-	A	-	-	-	-	-		-	-	-	-
<i>Micropsectra</i> sp.	A	A	-	-	-	-	-	-	-		-	-	A	A
<i>Polypedilum trigonus</i>	-	-	-	A	-	-	-	-	-		-	-	-	-
<i>Endochironomus subtendens</i>	-	-	A	A	-	-	-	-	-		-	-	-	-
<i>Einfeldia paganus</i>	-	A	A	-	-	-	-	-	-		-	-	A	A
<i>Limnophyes</i> sp.	A	A	-	-	-	-	-	-	-		-	-	A	-
<i>Cricotopus tricinctus?</i>	-	A	-	-	-	-	-	-	-		-	-	-	A
<i>Cricotopus</i> sp.	A	A	A	-	-	-	-	-	-		-	-	A	-
<i>Acricotopus</i> sp.	-	-	-	-	-	-	-	-	-		-	-	-	A
<i>Ablabesmyia</i> sp.	-	A	A	A	-	-	-	-	-		-	-	-	A
Arthropoda - Insecta - Diptera - Dixidae														
<i>Dixa</i> sp.	A	-	-	-	-	-	-	-	-		-	-	-	-
Arthropoda - Insecta - Diptera - Dolichopodidae														
<i>Dolichopus</i> sp.	A	-	-	-	-	-	-	-	-		-	-	-	-

Chordata - Vertebrata - Aves (Cont'd)	1967								1968					
	M	J	J	A	S	O	N	D	J	F	M	A	M	J
<i>Spatulata clypeata</i>	-	+	-	-	-	-	-	-	-		-	-	+	+
<i>Aythya americana</i>	-	+	-	-	-	-	-	-	-		-	-	-	-
<i>Aythya affinis</i>	+	+	+	-	-	-	-	-	-		-	-	+	+
<i>Porzana carolina</i>	-	+	-	-	-	-	-	-	-		-	-	-	+
<i>Fulica americana</i>	+	+	+	+	+	-	-	-	-		-	-	-	-
<i>Totanus flavipes</i>	-	+	-	-	-	-	-	-	-		-	-	+	-
<i>Chlidonias niger</i>	+	+	+	-	-	-	-	-	-		-	-	-	-
Chordata - Vertebrata - Mammalia														
<i>Ondatra zibethicus</i>	-	-	-	+	+	+	-	-	-		-	-	-	-

Provisional list of plants identified in the study area

Bryophyta - Musci

Philonotus sp.

Spermatophyta - Gymnospermae - Pinaceae

Picea glauca

Spermatophyta - Angiospermae - Monocotyledonae

Sparganium sp.

Glyceria grandis

Carex rostrata

Eleocharis palustris

Lemna minor

Lemna trisulca

Spermatophyta - Angiospermae - Dicotyledonae

Populus tremuloides

Salix sp.

Betula glandulosa

Betula papyrifera

Cerastium nutans

Ranunculus gmélini

Rubus sp.

Myriophyllum sp.

Ledum groenlandicum

Vaccinium vitis-idaea

APPENDIX II

Comparison of vertical sample and Ekman grab

Sample taken on May 26, 1969, at Sample Point IV

Taxon	Technique			
	V.S.		E.D.	
	#	#/m ²	#	#/m ²
Coenagrionidae	1	-	-	-
<i>Gyraulus parva</i>	33	-	10	-
<i>Physa heterostropha</i>	2	-	1	-
<i>Promenetus exacuus</i>	25	-	3	-
<i>Pisidium</i> sp.	-	-	2	-
<i>Helobdella fusca</i>	-	-	3	-
<i>Lumbriculus variegatus</i>	-	-	1	-
<i>Haliphus</i> sp. (Larvae)	-	-	3	-
<i>Candona</i> sp.	61	5,929	84	3,636
<i>Cyclocypris alma</i>	2	-	-	-
<i>Palpomyia</i> sp.	1	-	8	-
Tanypodinae	46	4,471	43	1,861
Chironominae (pupae)	2	-	9	-
Chironominae (larvae)	88	8,553	188	8,137
	g/sample	g/m ²	g/sample	g/m ²
Dry weight biomass of Chironomidae	0.013	1.264	0.0214	0.927

APPENDIX III

Additional water temperature data

Date 1967	Time	Temperature °C	
		Mud	Surface
May 19	14.40	14.8	15.0
24	10.15	14.0	14.0
26	14.50	15.1	15.1
June 8	15.00	21.2	19.5
12	09.45	-	22.0
20	12.15	19.6	20.2
27	10.15	19.8	20.6
29	11.00	18.2	19.0
July 8	09.45	21.5	22.0
11	09.45	22.0	21.0
13	09.45	18.0	17.8
16	09.20	19.6	19.6
19	10.00	-	18.5
29	10.30	22.0	22.3
Aug. 1	09.30	16.2	16.5
3	10.00	22.3	22.0
6	12.15	22.6	22.2
9	09.00	21.2	21.5
12	10.30	25.5	24.8
15	09.30	21.2	21.2

APPENDIX IV

Additional chemical determinations

Date	Test	Result
October 26, 1967	Chlorine	0.03 ppm
	Chromate	0.0 ppm
	Copper	0.0 ppm
	Hydrogen sulphide	0.0 ppm
	Silica	1.46 ppm
March 6, 1968	Silica (centre)	0.78 ppm
	Silica (east edge)	0.56 ppm

APPENDIX V

Chemical composition of snow - December 30, 1967

Test	Result
Calcium hardness	0.0 ppm
Magnesium hardness	7.0 ppm
Total hardness	7.0 ppm
pH	8.05 ppm
$\text{CO}_3^{=}$	0.0 ppm
HCO_3^{-}	8.0 ppm
Turbidity	15 JTU
Specific conductance	<50 $\mu\text{mhos}/\text{m}^2$
Orthophosphate	0.07 ppm

APPENDIX VI

*Comparison of temperature, wind and sunshine data for
the summer months of 1967 and 1968 with long-term averages*

Month	Temperature °F				Total Wind Mileage		Duration of Bright Sunshine	
	Mean 67-8	Max. Ave.	Mean 67.8	Min. Ave.	1967-8	Ave.	67-8	Ave.
<u>1967</u>								
June	67.6	68.5	47.7	47.0	6947	7067	282.4	255.1
July	74.8	74.4	53.4	51.7	7053	6557	310.2	309.3
Aug.	77.2	71.3	55.2	48.6	6659	6216	344.0	269.0
Sept.	73.5	62.6	48.1	40.4	6955	6513	247.6	187.3
Oct.	50.2	51.6	34.9	30.7	7466	6601	143.6	159.4
Nov.	35.9	32.2	20.8	16.8	6749	5880	127.5	100.8
<u>1968</u>								
March	41.6	31.0	26.4	13.2	6713	6619	163.0	166.9
April	50.5	50.0	29.4	28.9	7417	7490	244.4	221.7
May	63.0	63.6	41.2	40.5	9085	7871	333.6	267.4
June	68.2	68.5	48.0	47.0	7258	7067	257.4	255.7
Total :					72302	67881	2453.7	2192.6
% Increase :					6.5		11.9	

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